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CONCURRENT INBREEDING AND SELECTION IN THE DOMESTIC FOWL

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Received 26.vii.52

HETEROSIS has played a vital part in improving agricultural products. Long utilised to particular advantage in corn (review by Sprague, 1946), heterosis is becoming of increasing importance in certain other plants (Ashton, 1946), swine (Dickerson, Lush and Culbertson, 1946), and poultry meat (Jull, 1952). More recently, its use for egg production has been studied in the chicken (Warren, 1950 ; Bell *et al.*, 1952).

Despite the number of inbreeding and crossing experiments reported, the genetic mechanism responsible for heterosis and the origin of this mechanism by natural selection during the course of evolution is not understood. Selection experiments such as those of Mather and Harrison (1949) and Lerner and Dempster (1951), investigations of natural populations by Dobzhansky (1947, 1950) and others, and detailed studies of such polygenic traits as extra venation in *Drosophila* by Dubinin (1948) and crooked toes in chickens by Hicks (unpub.) have helped us. The majority of such studies, however, do not consider all of the three primary forces acting on domestic animals and plants ; viz. natural selection, artificial selection, and inbreeding.

The present paper deals with the first phase of an experiment on the effects of concomitant inbreeding and selection in the chicken, permitting to make some inferences as to the nature of the genetic system and the forces involved in its maintenance or deterioration.

I. CHARACTERS STUDIED

The characters analysed are (1) those which served as the criterion of selection, and (2) others for which the nature of response to inbreeding and indirect selective forces was studied.

Characters selected directly :—

(*a*) *November egg weight.* Mean weight of all eggs laid during November of the first year of lay.

(*b*) *November egg number.* Total number of eggs laid during November of the first year of lay.

(*c*) *November egg mass.* Product of November egg number and November egg weight. In each line direct selection was applied to only one component, either egg number or egg weight, but not both.

Other characters :—

(*d*) *Spring egg weight.* Mean weight of all eggs laid in a five-day period at the beginning of each of the months of March and April. In 1951, the mean weight of five eggs laid in April was used.

(*e*) *Six weeks body weight.*

(*f*) *December body weight.* Adult body weight (approximately at 8½ months of age).

(*g*) *Shank length.* Length of the shank measured in December.

The heritability of November and April egg weight in the production-bred flock has been estimated by Lerner and Cruden (1951) at approximately 0·60. November egg number has not been analysed in detail in the production-bred flock, but studies on other measurements of egg number (Lerner and Hazel, 1947 ; Lerner, Cruden, and Taylor, 1949) indicate that it should respond to mass selection.

The relationship between the two primary criteria of selection, November egg number and egg weight, is not well known. Rate of lay and egg size for the November to February were negatively correlated in a study by Taylor and Lerner (1938), while Blyth (1952) found such a negative correlation exists only at higher levels of laying (based on March production of Brown Leghorns).

Egg weight and body size in general are closely correlated. The genetic and phenotypic correlations between November and April egg weight were found to be 0·91 and 0·65 respectively (Lerner and Cruden, 1951). The same authors found a phenotypic correlation of 0·539 between December body weight and November egg weight. Two genetic correlations were given, 0·456 based on combined sire and dam components and 0·941 based on the sire component alone. A maternal effect on December body weight of 0·15 was found indicating that the genetic correlation based on the combined sire and dam components may be subject to error. The relationships between November egg weight and shank length has not been specifically studied. Lerner (1946) found that the phenotypic correlations of shank length with beginning egg weight (mean weight of the first 10 eggs laid) and January egg weight were 0·29 and 0·30 respectively, while the phenotypic correlation between shank length and December body weight was 0·52.

2. EXPERIMENTAL DESIGN AND MATERIALS

Eight inbred lines of chickens were established from the 1944 generation of the University of California production-bred flock (Lerner, 1950). Artificial selection was practiced for a single character in each line. The respective characters under selection in the lines were as follows :—

Line	Character selected	Direction
HNP	November egg number	High
HNM	,, ,,	High
LNP	,, ,,	Low
LNM	,, ,,	Low
HWP	November egg weight	High
HWM	,, ,,	High
LWP	,, ,,	Low
LWM	,, ,,	Low

When speaking of a pair of lines selected for the same character in the same direction (or of reciprocal crosses between two such lines) only the first two letters will be used ; *e.g.* the symbol HN includes HNP and HNM. Full designation of the parental lines will be given when referring to a single cross, the sire's line being given first.

Pullets were selected on the basis of their own record, with occasional consideration given to sister performance. Since dams, selected on the basis of their daughters' records were occasionally used, the average inter-generation span was somewhat higher than one year. Only year-old sires, selected on the basis of their sisters' records, were used.

A considerable reduction of selection pressure occurred in the latter part of the experiment. The number of offspring per dam surviving until breeding age decreased as inbreeding increased (Düzgünes, 1950) necessitating selection of a larger proportion of the available population. Furthermore, disease outbreaks occurred in the fall of 1949 and 1950 (Lerner, Taylor and Beach, 1950 ; and unpublished) which seriously affected November egg number and to some extent November egg weight. The disease in 1949 also lowered hatchability of affected birds in later mating seasons, further reducing the number of offspring in the succeeding generation. These factors led to the ultimate extinction of one line (LWM).

Rapid increases in the computed coefficients of inbreeding were obtained by restricting the size of the breeding population within each line to a single sire mated to several dams. Twelve to fourteen females per line were used as dams for each of the first four generations after which the number was reduced to six to eight females to permit making crosses. The numbers of pullet offspring and their mean coefficients of inbreeding in each line are given in table 1.

The production-bred flock (Lerner, 1950) served as a non-inbred control. Selection for various egg production characters, chiefly high hen-housed average egg-number (production index) for the first year of lay and high spring egg weight, was practiced in this flock (Lerner and Dempster, 1951).

Within the inbreeding experiment the lines selected for egg number served as inbred controls for egg weight. Similarly, the lines selected for egg weight served as inbred controls for egg number. Because of correlated changes in these two characters, the controls are not entirely independent of the experimental lines.

Reciprocal crosses between lines selected for the same character in the same direction were made in each of the last three years of the experiment (1949-51) except for LWP×LWM in 1951, omitted because of lack of LWM females. In 1951, additional crosses were made between lines selected for the same character but in opposite directions (HN×LN and HW×LW) and between lines selected for different characters but in the same direction (HN×HW and LN×LW).

TABLE 1

Computed inbreeding coefficients (F) of birds alive 1st December of year of hatch

Line	Year of hatch													
	1945		1946		1947		1948		1949		1950		1951	
	No.	F	No.	F	No.	F	No.	F	No.	F	No.	F	No.	F
HNP	73	0	44	17·6	52	33·2	24	42·4	31	49·1	9	47·3	9	55·9
HNM	85	0	16	18·0	65	31·6	21	44·7	42	52·3	22	57·5	8	62·4
LNP	54	0·2	50	18·7	53	30·0	11	36·0	42	38·4	44	39·0	28	48·6
LNM	25	0	32	12·5	25	26·0	24	35·2	23	43·5	37	48·4	9	52·9
HWP	53	0·5	76	15·7	37	24·3	52	23·2	34	32·0	15	33·3	20	41·4
HWM	46	0	34	13·9	19	27·8	19	36·8	15	39·8	18	48·0	10	52·7
LWP	56	3·5	34	11·2	29	27·3	24	33·4	17	47·6	31	49·0	11	58·1
LWM	61	0	61	17·5	70	26·9	15	38·7	13	43·0	3	40·3	0	...
Mean	453	0·52	347	15·88	350	28·92	190	34·13	217	43·25	179	45·82	95	50·88

Crosses were made by placing three to six females of one line in the mating pen with the male of the other line. Hence the same sire was used for propagation of his own inbred line and in crosses of that line with other inbred lines. A maximum of 14 dams was mated to one sire, six to eight of which were from his line and the remainder from other lines.

3. RESULTS

Only the results of November egg weight and number and December body weight in graphic form are presented here. The complete data on all characters studied are given in both tabular and graphic form in copies of the dissertation deposited in the library of the University of California at Berkeley.

November egg weight.—The effects of simultaneous selection and inbreeding on November egg weight are shown in fig. 1. There are six points that may be particularly noted.

First, rapid responses to selection in the four lines selected for high or low November egg weight were obtained during the early generations. Thus, in the third generation, the difference between

the means of the high and low lines was 12·2 gm. In the succeeding four generations no further response was observable in the HW lines. The LW lines, except for the brief period of plateau around the third generation, continued to decline an additional 3 gm. In the lines selected for November egg number, a correlated response of egg weight has occurred as expected from the negative correlation mentioned earlier. The difference between the means of the LN and HN lines was negligible during the first three generations and increased to only 2·2 gm. in the seventh generation (1951), in contrast to a difference of approximately 15 gm. between the HW and LW lines.

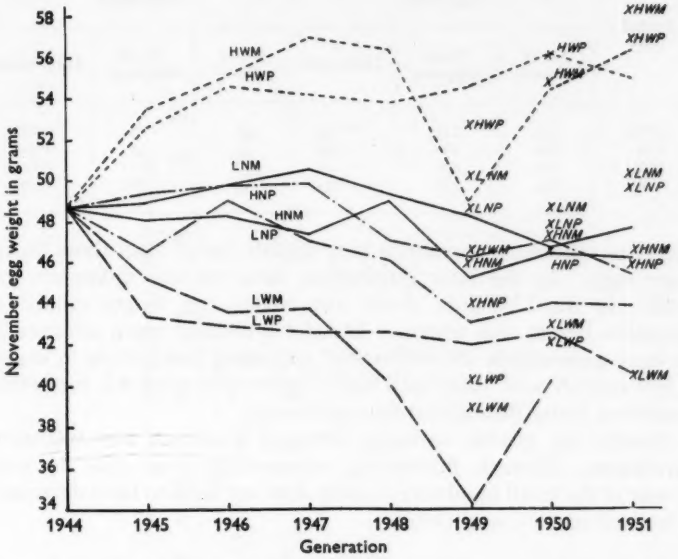

FIG. 1.—November egg weight in eight inbred lines and their crosses. Positions of crosses are marked by an X followed by designation of sire's line (dams are from the other line selected in the same manner as the sire's line). The LWM line was lost in 1950 from poor reproductivity.

Second, the means of the inbred controls (*i.e.* the four lines selected for egg number) have decreased in the later generations of the experiment. The mean November egg weight of the 1944 generation of the production-bred flock was 48·6 gm. During the first three generations the inbred control lines fluctuated around this value with a mean for the three years of 48·7 gm. In subsequent generations, a general decrease approximately equal in magnitude to that observed in the LW lines occurred.

Third, genetic homeostasis (Lerner, 1950) appears to be manifested. Lerner and Dempster (1951) failed to find evidence of any negative correlation between April egg weight and reproductive fitness in the

production-bred flock. However, selection for egg size in the production-bred flock was for an intermediate weight (Lerner, 1951) whereas the extreme deviates were selected in these lines. In the HW lines in the early generations the mean of dams weighted for the number of offspring produced was 0·074 gm. less than the unweighted mean of dams (table 2). Thus, dams laying smaller eggs

TABLE 2

Weighted (for number of offspring alive 1st December) minus unweighted means of dams for November egg weight

Pooled lines	1944-1946			1947-1950		
	No. of dams	No. of offspring	Difference	No. of dams	No. of offspring	Differences
HW	64	219	*−0·074*	48	129	*−0·288*
LN	62	215	*0·338*	37	53	*0·392*
HN	67	334	*0·140*	47	121	*0·132*
LW	69	292	*0·104*	44	76	*0·459*

tended to reproduce themselves only slightly better than those laying larger eggs. In the later generations, however, the difference was 0·288. In the LW lines, dams with higher egg weight tended to reproduce better, this tendency likewise becoming much stronger in the later generations, the differential increasing from 0·104 to 0·459. In HN and LN lines, dams with higher egg weights tended to reproduce themselves better throughout the experiment.

Fourth, the genetic variance, obtained from half and full sister correlations, although fluctuating considerably from year to year because of the small numbers involved, does not seem to have decreased as inbreeding continued (table 3).

TABLE 3

Genetic variance and heritability estimates for November egg weight

Lines	Genetic variance		Heritability	
	1945 and 1946	1948 and 1950	1945 and 1946	1948 and 1950
HW	1·9840	2·7444	*0·242*	*0·225*
LN	8·9516	(−11·0336)	*0·650*	*(−0·550)*
HN	0·8192	8·7548	*0·095*	*0·954*
LW	4·1744	7·1200	*0·471*	*0·787*

Fifth, the crosses occur in the relative order that would be expected from the assumption that gains from selection acting directly on egg weight, or indirectly as a result of the negative correlation between egg weight and egg number, have been realised in all lines. Thus

in all three generations in which crosses were made (1949-51) crosses between the HW lines were highest for egg weight followed in descending order by LN, HN, and LW. Furthermore, the additional types of crosses performed in 1951 lie in the order expected on the basis of the above assumption (fig. 2).

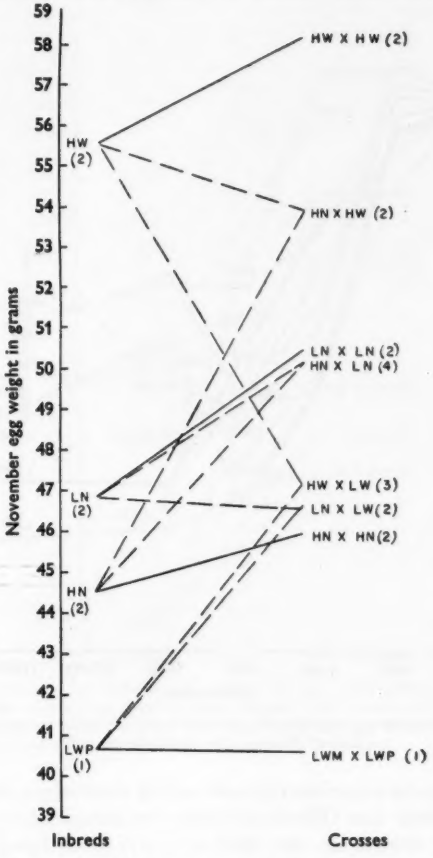

FIG. 2.—Relative values of inbreds and crosses of 1951 generation for November egg weight. The connecting lines between inbreds and crosses are drawn merely to facilitate interpretations. The numbers in parentheses represent the number of lines or line crosses (including reciprocal line crosses) pooled.

Sixth, means of crosses between lines selected for the same character in the same direction frequently are greater than the means of the parental inbred lines. In 1951, the year in which no disease outbreaks were experienced, the difference between inbreds and crosses was greatest for HW and LN. The HN crosses were only slightly superior

to the HN inbreds, whereas the LWM × LWP cross and LWP inbreds were approximately equal (there were no LWP × LWM crosses or LWM inbreds in this year).

November egg number (fig. 3). Severe inbreeding depression of roughly 12 eggs occurred in the second and third generations (1946 and 1947). Thereafter little or no change was evident.

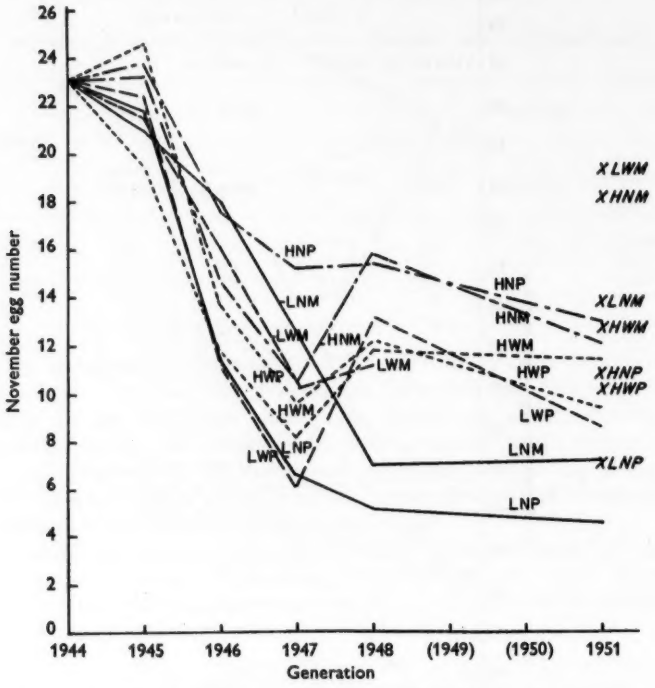

FIG. 3.—November egg number. No records were available in 1949 and 1950 because of disease. For description see fig. 1.

The effects of selection did not reveal themselves until the fourth generation when the HN lines finally became clearly differentiated from the LN lines with the HW and LW lines lying intermediate. Selection for egg weight did not result in differentiation between the LW and HW lines for egg number.

The crosses (figs. 3 and 4) are not as uniform for egg number as they were for egg weight. However, the means of the reciprocal crosses HN × HN, HW × HW, and LN × LN, are arranged in that order, although the order of the individual crosses is mingled. The single cross involving the LW lines (LWM × LWP) was exceptionally high.

Crosses between lines selected differently do not lie in the order

observed for egg weight. They generally exceeded the crosses between lines selected similarly (fig. 4). Thus the unweighted mean was 15·81 eggs for crosses between lines selected for the same character but in opposite directions, 14·01 for crosses between lines selected for different characters, and only 13·23 for crosses between lines selected for the same character in the same direction.

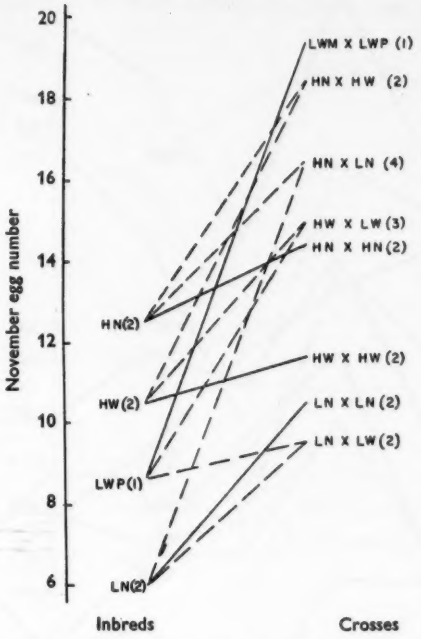

FIG. 4.—Relative values of inbreds and crosses of 1951 generation for November egg number. The connecting lines between inbreds and crosses are drawn merely to facilitate interpretations. The numbers in parentheses represent the number of lines or line crosses (including reciprocal line crosses) pooled.

In general, crosses tend to be superior to both parental lines, the exception being HWP×HWM which was intermediate and HNP×HNM and LNM×LWP which were lower than either parental line. The first two exceptions were crosses between similarly selected lines, the third being between lines selected for different characters.

The mean of all crosses is more than four eggs lower than the mean of the 1951 production-bred flock. Only one cross, LWM×HWM, exceeded the mean of the production-bred flock—by 0·2 of an egg.

November egg mass.—Results for egg mass were very similar to those for egg number. This is expected because changes in egg number contribute more to variation in egg mass than do changes in

egg weight. The only notable exception is that the HW lines and line crosses have higher values for egg mass than the HN lines in contrast to lower values for egg number.

Spring egg weight.—The results for spring egg weight were almost identical with those for November egg weight. Indirect selection

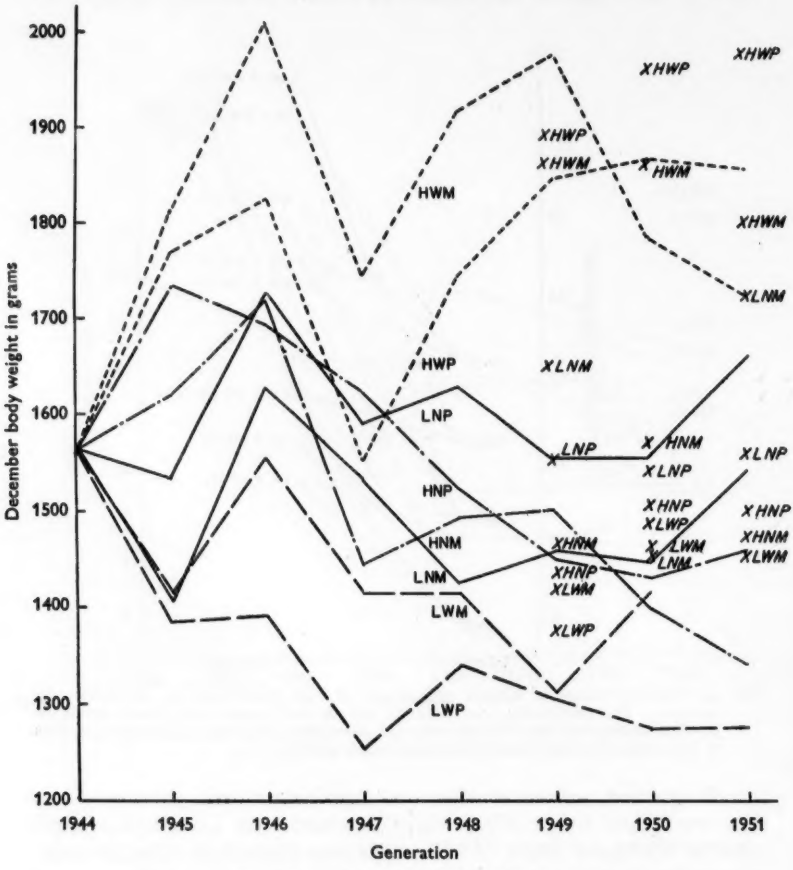

FIG. 5.—December body weight. For description see fig. 1.

was effective as expected in view of the genetic correlation between the two measures of egg weight. During the early generations the LN lines remained at approximately the level of the 1944 generation of the production-bred flock, the HN lines approximately 2 gm. lower. As in November egg weight, a decline occurred in the LN and HN lines in the later generations.

The failure of the crosses between lines selected (directly or

indirectly) for low egg weight to exceed the inbreds was even more striking for spring egg weight than for November egg weight in 1951. Thus the mean of HN crosses (47·9) was actually lower than the mean of the inbreds (48·3). The LWM×LWP was about equal the mean of the LWP inbreds in 1951 and the last known value (1950) for the LWM line.

December body weight (fig. 5).—The production-bred flock showed a large and consistent increase during the years 1944 to 1948 (from

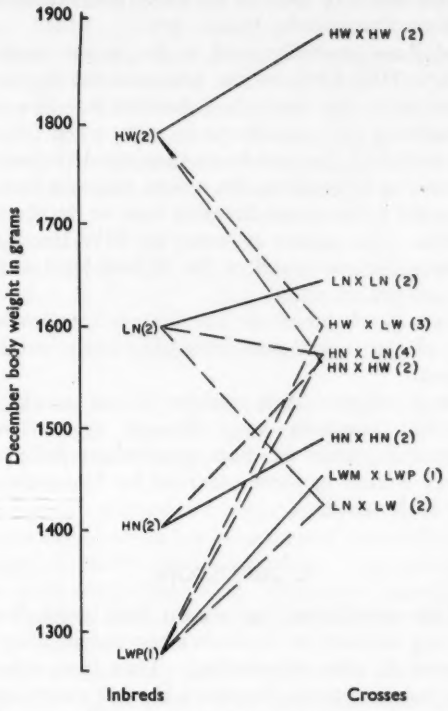

FIG. 6.—Relative values of inbreds and crosses of 1951 generation for December body weight (females only). The connecting lines between inbreds and crosses are drawn merely to facilitate interpretations. The numbers in parentheses represent the number of lines or line crosses (including reciprocal line crosses) pooled.

1563 to 1814 gm.) thereafter remaining relatively stable. Since body weight was not a criterion of selection, this rise is presumably a correlated response to selection for higher egg weight which was particularly intensified about 1946.

The effect of selection in the HW and LW lines closely parallels that observed for November egg weight. Virtually all of the response to selection in the HW lines was obtained in the first generation. Thereafter, body weight fluctuated around the same level later

attained by the production-bred flock. The LN lines showed a variable behaviour, LNP remaining relatively stable at a level slightly above the 1944 production-bred flock, while LNM was considerably below this level until the last generation when a sharp rise of nearly 100 gm. occurred bringing it back almost to the level of the 1944 production-bred flock. The LW lines show a more or less continuous decrease throughout the experiment. The HN lines also steadily declined, although at a higher level. The difference of over 200 gm. between the HN and LW lines in the early generations was reduced to roughly half that amount by 1951.

The inbred lines generally tend to lie in the same descending order (HW, LN, HN, LW) as was observed for egg weight, being exactly so arranged in the last (1951) generation. The crosses are in the expected order in all years except in 1950, when LN and HN are reversed, and the LNM line was lower than the LW lines.

As in the case of egg weight, the crosses between lines selected for the same character in the same direction tend to lie above the corresponding inbreds. The crosses between the HW lines lie at a level (1899 gm.) approximately equal to the highest level attained by the inbred lines (1908 gm. in 1949).

Shank length.—Shank length in the inbred lines tended to follow the behaviour of egg weight and December body weight with only minor exceptions.

Six weeks body weight.—Body weight at six weeks of age was analysed only for generation 1949 through 1951. The behaviour of inbred lines and crosses in these generations indicated that the effects were very similar to those observed for November egg weight and December body weight.

4. DISCUSSION

General.—This experiment has shown that gains from selection for November egg number or November egg weight may be obtained in lines subjected to close inbreeding. Thus lines selected for the same character but in opposite directions become clearly differentiated from each other. Differentiation for egg weight was evident in the first generation but was not observable for egg number until the fourth generation.

The apparent early ineffectiveness of selection for egg number appears to be due to the variable effects of inbreeding degeneration occurring in the second and third generations. As this decline became arrested, the effects of selection became evident.

All lines except those selected for high weight (HWP and HWM) showed some depression of egg weight in the later stages of the experiment after computed inbreeding coefficients of approximately 30 per cent had been attained. Waters (1941) observed a similar phenomenon.

In general, crosses were arranged as expected with reference to egg weight on the basis of artificial selection pressures in the parental lines. Thus the descending order of crosses between similarly selected lines was HW, LN, HN and LW. The crosses with respect to egg number in 1951 tended to follow the same behaviour. However, HNP×HNM was lower than LNM×LNP, an exception not unexpected in view of the predominance of environmental variations (low heritability).

Also, crosses in which the LWM sire was involved were exceptionally high. Thus, LWM×HWM and LWM×LWP, ranked first and third respectively among the 18 types of crosses performed. Unfortunately, no LWM females were available for crossing. The sire and dams from LWP behaved quite differently in crosses other than those with the LWM male. Hence, the unusual performance of the LWM male appears due to something peculiar to him rather than to a general characteristic of lines selected for low egg weight.

The HN×HW crosses clearly exceeded all other inbreds and crosses for egg mass. The LN×LW crosses were clearly lower for egg mass. This, however, is not a case of multiplicative gene action analogous to that in Powers' (1944) tomatoes because the majority of the effects at least are directly attributable to egg number. Thus, the crosses were in practically the same order for egg mass as for egg number.

Crosses between similarly selected lines tended to be superior to contemporary inbreds from the parental lines. This was true for the primary criterion of selection and also for those characters showing correlated response.

Correlated response.—Correlated response as a phenomenon characteristic of selection experiments has been treated in detail by Mather and Harrison (1949), Lerner (1950), and others. The present experiment adds further emphasis to this point. Computed correlations between the characters studied here have been presented in the section on the description of characters.

Correlated responses may not always be of a direct genetic nature. Thus, selection for egg number led to clear differentiation between the HN and LN lines with respect to egg weight, the LN lines having the higher egg weight (fig. 1). However, selection for egg weight in the HW and LW lines was not effective in changing egg number. This situation is somewhat analogous to that reported by Lerner (1946) in which body size (or sexual maturity) appeared to limit the expression of genes for egg weight. In the present case, both characters are manifestations of metabolic efficiency, or the capacity of the bird for the production of total egg mass. Changes in egg number in the HN and LN lines may have resulted in the differentiation of these lines for egg weight largely through limitation in the HN lines of the amounts of material available for each egg. This interpretation is in agreement with Blyth (1952), namely that egg number and weight

are correlated because the full genetic potential for egg size is not realised when the bird is laying at a high rate. The question here is whether the HN lines are laying at a sufficiently higher rate than the LN lines to account for the difference in egg weight. Egg number in the HW and LW lines would be expected to show some correlated response to selection for egg number. Small differences in egg number, however, would tend to be obscured by the larger magnitude of environmental variation.

Changes in November egg size were accompanied by corresponding changes in spring egg weight, six weeks body weight, December body weight, and shank length. These correlated changes appear to be of the magnitude expected on the basis of simple genetic correlations. Lerner (1950) gives the formula for estimating the expected changes in a correlated trait as :—

$$\Delta G_B = rG_AG_B \frac{\sigma G_B}{\sigma G_A} \Delta G_A$$

Where ΔG_A and ΔG_B are the genetic changes for the selected and correlated traits respectively (in this case, ΔG was replaced by the difference between lines), σG_A and σG_B are the square roots of the respective genetic variances, and rG_AG_B is the genetic correlation between the traits. The expected differences between the HW and LW lines for six weeks body weight and December body weight were calculated to be 72 * and 472 † gm. respectively as compared to observed differences of approximately 69 and 514 gm. in 1951.

Cryptic gains from selection.—During the early stages of the experiment it was possible to apply strong selection pressures for high and low November egg number. In later generations, particularly during the disease outbreaks in 1949 and 1950, very little selection pressure for egg number was possible. However, differentiation between the HN and LN lines (the lines selected for egg weight being intermediate) was not apparent until the fourth generation (fig. 3). Hence gains from selection must have been made during the earlier stages but were obscured by the severe inbreeding degeneration occurring at different rates in the various lines. Such gains from selection have been described as *cryptic* by Lerner (1950).

Similarly, gains from selection were not always apparent in the inbred lines with respect to the size characters. However, crossing the lines allows the gains from selection to be fully expressed. Thus the unweighted means of reciprocal crosses between similarly selected lines were arranged in the descending order HW, LN, HN and LW for all characters of size in all three years such crosses were performed,

* The values used to obtain this figure ($\sigma G_A = 1{\cdot}2$, $\sigma G_B = 13{\cdot}7$, and $rG_AG_B = 0{\cdot}42$) were computed by Dorothy Cruden Lowry from 1285 birds in the 1945, 1946, and 1948 hatched generation of the production-bred flock. The value for ΔG_A (15 gm.) was obtained from fig. 1.

† The values used to obtain this figure ($\sigma G_A = 2{\cdot}4$, $G_B = 80{\cdot}4$, and $rG_AG_B = 0{\cdot}942$) were obtained from Lerner and Cruden (1951) and unpublished data from the same analysis.

with the exception of six weeks and December body weights in the 1950 generation.

Induced heterosis for egg size.—The release of cryptic responses from selection by the crossing of inbred lines will result in the phenomenon of heterosis. Egg weight of the HW crosses increased during the three years crosses were made. The HW inbreds, however, remained at the plateau reached the year before the first crosses were made. Hence it seems likely that the heterosis appearing in 1951 was due to the fact that gains were being realised in the inbred lines in the later generations but were being nullified by the increasing effects of inbreeding. In the LN lines, in which there was only weak indirect selection for higher egg weight, the depressing effects of inbreeding were exhibited in the later generations. Crossing these lines returned egg weight to approximately the level shown by the inbred lines prior to the onset of the inbreeding depression. On the other hand, selection in the LW and HN lines was in the same direction as inbreeding depression. The crosses were approximately equal to or only slightly higher than the inbreds ; and in one instance, HN with respect to spring egg weight in 1951, the crosses were below the inbreds. It appears that gains from selection were expressed in the inbreds as well as in the crosses, these gains in some cases being augmented by an additional effect of inbreeding depression. It remains to be seen in future generations whether the crosses eventually will fall below the inbreds.

Dobzhansky (1948) explains heterosis induced by natural selection in wild populations of *Drosophila pseudoobscura* on the basis of co-adaptation of the genic contents of chromosomes differentiated by inversions. The heterosis observed here in the HW lines has also arisen through the action of selection. However, it cannot be explained in the basis of co-adaptation because the lines have been isolated from each other. Heterosis in this case appears to be associated with metabolic efficiency. Egg weight depends on the availability of metabolic materials for maximum expression. As metabolic efficiency is decreased by inbreeding, egg weight in turn is depressed. The restoration of metabolic efficiency by crossing lines permits full realisation of the cryptic gains from selection for egg weight.

Optimal egg weight.—It is possible that the decline noted in the HN and LN lines during the latter stages of the experiment was due to natural selection rather than inbreeding. Artificial selection for higher egg weight in the production-bred flock, although not for the extreme deviates, nevertheless has resulted in the mean being higher than the optimal value for this flock (Lerner and Gunns, 1952). Relaxation of artificial selection in lines (HN and LN) derived from this flock should result in a return to the optimal level under the action of natural selection. The unweighted mean of these lines during the first three generations was relatively stable and approximately equal (48·70) to the 1944 production-bred flock (48·60).

Thereafter, a consistent decline was observed which could be attributed to natural selection for an optimum at or below the level reached by these lines in 1951 (45·75 gm.). Lerner (1951) and Lerner and Gunns (1952) computed the optimum to be 46·29 gm. by fitting second degree polynomials to data obtained from a sample of 189 birds in the 1950 production-bred flock. The mean of the HN and LN inbreds in that year (46·00) is in close agreement. Under such a view, natural selection for optimal egg weight and artificial selection for high egg weight are in equilibrium in the HW lines whereas in the LW lines, gains to artificial selection are still being obtained although the pressure of natural selection is increasing (table 2).

On the other hand, if inbreeding were responsible, the crosses rather than the inbreds would be expected to yield the valid estimate of the optimum. The mean of the crosses in 1951 was 48·20 gm., a value considerably above that of the inbreds. There are several reasons why the optimum computed by Lerner and Gunns may be too low with the 1951 crosses furnishing the best estimate.

1. The computed optimum was obtained from 1950 records, one of the two years in which disease outbreaks depressed November egg weight. The mean of crosses between number lines in that year was 47·42 gm. which is roughly halfway between the 1951 crosses and the computed optimum.

Furthermore, the disease outbreak in 1949 had a severe effect on egg number and also on egg weight particularly in certain lines (HWM and LWM). In general the crosses were more resistant to this disease than the production-bred flock (Lerner, Taylor and Beach, 1950). Although a similar study was not carried out for the disease epidemic in 1950 it is possible that the crosses were again more resistant. Consequently November egg weight may have been depressed more in the 1950 production-bred flock than in the crosses. Hence the disease may account for more than half of the difference.

2. The November egg weight used by Lerner and Gunns (1952) was based on the first five eggs laid in November whereas data in this experiment are based on all eggs laid during November. Since egg weight increases during this period, part of the difference may be accounted for by the difference in definition of the character.

3. The computed value was determined for fitness as measured by the number of offspring at the day-old stage, while the observed values refer to the number of offspring surviving to eight months of age.

4. Special hatchability tests similar to those of Lerner and Gunns (1952) were carried out in these lines in 1951 by C. A. Gunns and Dorothy C. Lowry. The results obtained (unpublished) indicate that in the number lines, optimum egg size for hatchability was above the means of the respective lines. Optimum egg size was below mean egg size in the HW lines as expected. The data were too limited for conclusive results in the LW lines.

The discrepancy between the computed and observed (from crosses) optimums in no way invalidates the conclusions reached by Lerner (1951) that the optimal value of egg weight with respect to fitness lies below the mean of the production-bred flock. In fact, these data strengthen that view, the optimum estimated from 1951 crosses being 3·0 gm. below the mean of the production-bred flock(51·2 gm.)

Balance for fitness.—Düzgünes (1950) noted that there was selective elimination of the relatively more homozygous individuals in the lines studied here, suggesting the presence of a balance mechanism for fitness. Shultz and Briles (1953), by using genes involved in the production of cellular antigens as markers, demonstrated the effectiveness of selective forces in maintaining balanced polymorphism in these lines, in four additional inbred lines, and in the relatively non-inbred production-bred flock. The results presented here are further evidence for the existence of a balance mechanism.

The responses to direct selection for high and low November egg weight had virtually ceased by the third generation. No noticeable decrease in the genetic variance from inbreeding was observed (table 3). It was found, however, that natural selection was acting in favour of an intermediate egg weight. Thus in the HW lines, dams with smaller egg size reproduced themselves better whereas in the LW lines the dams with higher egg weight reproduced themselves better (table 2). These differences were greater in the generation during which the lines were plateaued than during the earlier generations when gains were being obtained.

Hence, the presence of an optimum egg weight appears to be due to an association of egg weight with the balance mechanism for fitness. The greater the deviation of egg weight of the population from the adaptive peak, the stronger are the forces of natural selection which tend to restore balance for fitness. This negative correlation between fitness and the deviation of a selected character from the optimum has been previously demonstrated in a line of chickens selected for long shanks by Lerner and Dempster (1951), much as expected on the basis of Mather's (1941) theory of polygenic balance.

The behaviour of November egg number also is suggestive of a balance mechanism. This trait was characterized by severe inbreeding degeneration (fig. 3) in the second and third generations in which mean levels of inbreeding of 0·16 and 0·29 were attained. No further general decline in egg number occurred although the computed inbreeding coefficient increased to over 0·50 in the next four generations. Artificial selection for high egg number was not sufficient to prevent the severe decline although it did result in a higher equilibrium level in the HN lines than in the other lines.

Unless there is a threshold level of homozygosity beyond which no further detrimental effects occur, an unlikely possibility, one must assume that some force becomes effective in arresting the decline. The only possible force appears to be natural selection. Thus con-

tinuous inbreeding pressure acting towards homozygosity with the resulting disruption of balance for fitness is opposed by strong natural selection in favour of the heterozygotes.

Crossing lines will tend to restore balance disrupted by inbreeding. If a character depends to large extent on a balance mechanism, its expression in crosses will depend on the degree to which such balance is restored. It might be expected that crossing two inbred lines in which selection has acted towards greater genetic differentiation will tend to restore balance to a greater extent than crossing two lines in which selection has acted towards genetic similarity. This may be the explanation for the superiority of November egg number of the crosses between differently selected lines over crosses between similarly selected lines. This same situation also was noted for egg weight but only to a slight extent. The reverse is true, however, for December body size.

5. CONCLUSIONS AND SUMMARY

On the basis of the data obtained, some inferences as to the nature of the genetic system operating in this material can be made. The pertinent observations are outlined below.

1. A reduction in reproductive fitness in the eight lines due to inbreeding has occurred (Düzgünes, 1950). This effect led to a decline in the amount of selection pressure that could be practiced. Disease epidemics in 1949 and 1950 (5th and 6th generations), further reduced the effectiveness of artificial selection.

2. Close consanguineous mating caused a decline in November egg number in the second and third generations, no further decline occurring in the next four generations even though the degree of inbreeding greatly increased.

3. A decline in November egg weight began coincident with the cessation of the degeneration in egg number and continued throughout the duration of the experiment.

4. Differentiation between lines selected in opposite directions for egg number did not become apparent until the fourth generation when inbreeding degeneration ceased, although the most effective selection pressures had been applied in the previous generations.

5. Responses to selection for egg weight were immediately apparent. These visible responses ceased by the fourth generation.

6. Within lines, dams whose egg weight was closer to the optimum tended to reproduce themselves better (table 2).

7. The behaviour of egg mass (weight multiplied by number) was almost identical to that of egg number.

8. Differentiation with respect to egg number between the lines selected for high number (HN) and low number (LN) was accompanied by a correlated differentiation of these lines with respect to egg weight. The reverse was not noticeable in the lines selected for high and low egg weight (HW and LW).

9. Correlated response of spring egg weight, six weeks body weight, December body weight, and shank length with November egg weight was noted. Changes in body weight were of the magnitude expected on the basis of simple genetic correlations between characters.

10. The ranking with respect to mean egg number of crosses between lines selected for the same character in the same direction was essentially that expected on the basis of selection for egg number. Crosses were generally superior to the contemporary inbreds, but did not exceed the production-bred flock from which the inbred lines were derived.

11. The means of crosses with respect to egg weight fell in the order of magnitude expected on the basis of additive gains from selection. These crosses were superior to the mid-values of the contemporary inbreds from the parental lines.

12. Crosses between lines selected differently tended to be superior to crosses between similarly selected lines. This was especially true for egg number and to some extent for egg weight but not for December body size.

It is apparent that the genotype is not simply a collection of independently acting genes. Rather it is an integrated complex which has arisen during the course of evolution under natural selection acting on an essentially heterozygous system. The characters studied here are but more or less interrelated manifestations of the general underlying physiological organisation and should be considered in part as indicators of the condition of that organisation. Thus egg number and egg weight are correlated manifestations of metabolic efficiency. The negative correlation between them exists only at higher rates of production where the ability of the bird to produce sufficient metabolic products for maximum expression of both characters is exceeded (Blyth, 1952). The relationship, however, is not adequately expressed simply as the total egg mass produced as shown by point 7 above. Similarly, the size characters studied can be considered to be manifestations of a basic physiological condition as shown by the correlated responses to changes in egg weight.

Interpretation of these results requires a consideration of three forces—natural selection, artificial selection, and inbreeding. The action of these forces produces changes in the genetic composition of a population until an equilibrium between them is reached. This results in an apparent stability of the mean of the population. Further observable changes are then dependent either on an alteration of the relative pressures of these forces or on fundamental changes in the genetic structure. However, the underlying genetic basis for the equilibrium may be changing even though such changes are not reflected on the phenotypic level.

These data furnish three illustrations of the establishment of an equilibrium. First, the rapid decline in November egg number to a lower stable level appears best explained on the basis that inbreeding

disrupts the heterozygous balanced genetic system for fitness. The increase in homozygosity is opposed by natural selection and an equilibrium is reached as a result. That artificial selection has also played a part is clearly shown by the fact that the lines selected for high and low number plateaued at a higher and lower level respectively than the inbred-control lines which were not selected for egg number. These gains were in part cryptic during early generations finally becoming apparent when further inbreeding degeneration ceased.

The plateau shown by November egg weight in the HW lines furnishes the second example. Part of the cessation of gains from selection for high egg weight was due to the opposition of natural selection, as demonstrated here by the fact that dams with lower egg weight reproduced themselves better. It appears, however, that some gains were being realised during the plateau period but were cryptic owing to a counterbalancing depressing effect of inbreeding. Removal of the depressing effect of inbreeding by crossing allowed the expression of the cryptic gains from selection resulting in the heterotic behaviour of the HW crosses. The HN and LN lines (in which the primary selective force was natural selection towards the optimum) exhibited inbreeding degeneration. On crossing these lines, egg weight was restored to the optimal level.

The third example is the behaviour of egg weight in the LW lines. The short plateau around the third generation apparently represents an equilibrium between artificial and natural selection. Thus dams with higher weight reproduced themselves better (table 2). In later generations despite an increase in the pressure of natural selection for higher egg weight, further decreases were obtained presumably by the joint action of artificial selection and inbreeding. Crossing the lines restored egg weight to the level of gains from selection, in this case slightly below the plateau level of the third and fourth generations.

Thus natural selection tends to maintain the heterozygous system characteristic of the adaptive peak established during the course of evolution. Artificial selection and inbreeding as encountered in the improvement of domestic animals will tend to disrupt this balanced genetic system with a decrease in the metabolic efficiency and reproductive fitness characteristic of that adaptive peak. It may be expected then, that computed inbreeding coefficients will overestimate the actual amount of homozygosity achieved as indicated previously by Düzgünes (1950) and Shultz and Briles (1953) for this material, and by Mather (1950) in a more generalised fashion. Furthermore, genetic gains as a result of artificial selection for a character (*e.g.* egg weight) dependent for its maximum expression on an efficient physiological system may not be apparent on the phenotypic level. Restoration of the heterozygous system by crossing allows the expression of these cryptic gains.

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MARCH EGG NUMBER IN INBRED AND FIRST CROSS BROWN LEGHORNS

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In the course of an earlier study (Blyth, 1952) the frequency distribution of pullets, on the basis of March egg numbers, was found to be negatively skewed, the curve approaching normality in shape for birds laying more than 18 eggs but tapering out in a long thin tail of less productive individuals. It was concluded that this resulted from the presence of two component types of variation—a basic maximum rate of laying (closely associated with egg weight), and irregularities superimposed upon it by gaps of varying length in the sequence of laying. There was some indication that the incidence of this *pausing* differed characteristically in the three inbred lines compared, and that it had increased between the two periods studied (1935-39 and 1945-49). The conjecture was also made there that pauses may depend on factors divorced from the direct process of egg formation. Lack of constitutional vigour might bring about such effects for, though difficult to pin down to particular causes, it must have its origin in shortcomings of development and function. Greenwood and Blyth (1948) have noted a tendency for different organ weaknesses to segregate in the isolate groups of the same Brown Leghorn flock; they inferred that the lowered mortality they encountered in first crosses might have resulted from the introduction of complementary desirable genes from the two parental lines, covering up each other's deficiencies.

While it cannot be assumed offhand that gaps in March production bear any relation to the well recognised interruptions of moult, broodiness and winter pause, it seems not unlikely that their incidence should reflect the birds' ability to withstand the more random environmental stresses that fall upon their ovarian activity throughout the year. Further examination of the March data available has therefore been made to learn how the variability in a successful interline cross compares with that in its parental types; whether, in fact, improvement in egg production comes about through a rise in rate, or reduction in irregularities in this rhythm, or both. Direct genetic effects on egg numbers could be expected to result in the F_1 mean being intermediate, or lying near that of one or other of the ancestral types, but it is unlikely that they would give rise to a decrease in pausing below that of the superior parental line; this would be a probable consequence however if degenerative deficiencies were influencing production as suggested above.

The cross under discussion was made a number of times in different years ; the annual progeny groups are small and their arrangement is unsuited to rigorous statistical comparisons ; the mean value for each has therefore been presented separately to display the level of consistency among them. Of the two parental lines, one is a general purpose stock, (B), selected for a number of economic traits, while in the other, intensity (I), the emphasis has been solely on intensity of production. March records for both are described in the original publication. Information about the numbers of birds in the subsequent comparisons, and the years in which they were hatched, are given in table 1 ; in designating the reciprocal matings the initial

TABLE 1

Number of pullets per group

Group	1938	1944	1946	1947	1948	Total
B	73	69	59	73	79	353
IB	16	...	...	38	22	76
BI	...	24	10	19	22	75
I	19	29	42	32	38	160

letter of the dam's line is given first. All the annual samples of the crosses were from single pen matings except the small 1946 one which derived from two cocks ; the average yearly number of cocks used in the lines was four for B and two for I. A more general comparison of traits in these crosses and the participant lines has been made by Greenwood and Blyth (1951).

Rate.—The method of exposing differences in rate used before was to compare groups after eliminating birds falling below certain levels of production (18, 22, or 24 eggs). Such a measure is obviously only approximate but the reliability of possible alternatives is equally unknown so it is the first procedure used again here, with 22 eggs as the lower limit. In table 2 the mean egg number for this class is contrasted with that for all pullets in the samples of reciprocal first crosses and the representatives of their parental lines hatched in the same years. The general means for the complete populations indicate superiority of the reciprocals over both parent types, and only in one of the separate samples does this not hold true : there, in 1938, the cross had a B sire (IB) and falls in an intermediate position. Among the curtailed classes (table 2B) the higher position of the crosses is no longer maintained : they still exceed B though the range of variation is now smaller, but are indistinguishable from I in performance.

The difference in the levels of the corresponding means in the two tables is not necessarily wholly accounted for by the inclusion in the first of birds with production gaps : pausing individuals may

also be intermingled with non-pausing higher producers. It was the supposition that this occurred that led to placing the arbitrary line of division so high. Such an arrangement of course has the concomitant disadvantage that it may be eliminating too large a proportion of pullets which are laying at a low basic rate, and so unbalancing some of the frequency distributions. It is quite conceivable, for instance, that inherent rates yielding less than 22 eggs in the month occur : a bird laying every other day could only produce 15 or 16 eggs ; on the other hand birds with high potential rates could miss several consecutive days without falling below the limit

TABLE 2

Mean number of eggs in March

Group	1938	1944	1946	1947	1948	Total
2a. All Birds						
B	21·0	22·1	15·6	23·1	19·3	20·35
IB	23·2	...	...	24·4	25·1	24·33*
BI	...	24·7	21·2	24·3	22·5	23·47*
I	24·0	24·1	19·6	23·3	22·0	22·27*
2b. Birds Laying 22 or more						
B	23·2	23·7	22·9	24·5	23·6	23·80
IB	23·4	...	...	25·1	25·4	24·82*
BI	...	24·9	25·3	25·4	23·7	24·78*
I	25·2	25·0	24·5	25·1	24·9	24·94*

* t test for correspondence with B mean has a probability $<0{\cdot}001$.

adopted. In the first case there would be an overestimate of the mean in groups which contained many individuals with a genetically low rate of laying, while the second contingency could act in the opposite direction. The only test of this which it seemed worthwhile undertaking on the present restricted data was that made by eliminating all birds with gaps greater than a single day. This classification may be affected by the distribution of unrecorded (floor) eggs but these did not exceed 2 per cent. of the total, were usually below 1 per cent., and did not appear to be abnormally distributed among the samples.

When the means were recalculated in this way they differed little from those for the 22-up samples except in B groups where the difference was always negative, and resulted in a decrease of about half an egg in its general mean to 23·14 eggs ; the comparable figures for the others were, IB, 24·98 ; BI, 24·75 ; and I, 24·84 eggs, and their individual year samples all differed significantly from corresponding B means except I 1947 and BI 1948. This suggests that while the first method of determining basic rate was satisfactory for

the last three groups, it eliminated more B birds which laid at a naturally low rate, and so overestimated the mean there.

The proportion of pullets in a sample which lay less than 22 eggs (table 3) also demonstrates that B differs from the others but again does not distinguish between variations due to rate and those in the

TABLE 3

Percentage laying less than 22 eggs

Group	1938	1944	1946	1947	1948	Total
B . . .	51	26	83	20	63	48
IB . .	6	...	...	8	5	7
BI . .	...	4	30	16	36	20
I . . .	16	10	59	19	37	32

incidence of deviations from it; half the B birds fall below the arbitrary division line; only about a third of the I group do so, and still less of the crosses. As there are only two direct comparisons available between the reciprocal samples (1947 and 1948) the tendency for IB to rank slightly better than BI on mean performance, which manifests itself in this and the following table, will merely be noted here without comment.

Pausing.—Non-genetic fluctuations in the basic maximum rate may occur both seasonally and in adverse environments such as a late snowstorm encountered by 1946 hatched pullets in the following

TABLE 4A

Percentage with gaps over 1 day

Group	1938	1944	1946	1947	1948	Total
B . . .	36	22	71	34	65	45
IB . .	13	...	...	32	14	22
BI . .	...	25	40	42	27	32
I . . .	42	27	62	44	50	47

March. These as well as unrecorded eggs might upset calculations of the number of missed potential laying days. The proportions of pausing birds therefore have been set out for two levels: those with maximum gaps of over one day, and over four days, irrespective of the number of eggs they lay. In table 4A the first of these classifications, while showing an overall smaller proportion of crosses with gaps exceeding a single day, does not differentiate very well between them and the inbreds within particular years. In table 4B, however, the absence of longer pauses in the former is more striking; in actual numbers, only one IB and three BI birds stopped for more than

four days while 29 I and 66 B did so. Comparison of the two halves of the table gives the impression that there may be no real difference between the crosses and the lines in regard to smaller interruptions and that it is mainly the incidence of larger ones that is affecting the annual production average.

TABLE 4B

Percentage with gaps over 4 days

Group	1938	1944	1946	1947	1948	Total
B . . .	9	10	52	6	23	19
IB . .	0	...	...	3	0	1
BI . .	...	0	20	5	0	4
I . . .	0	7	38	19	13	18

A new point emerges here about the two inbred lines; though relatively fewer I than B pullets were found to fall below the 22 egg limit (table 3), the percentage of long and short pauses is roughly the same in both. This casts doubt on the inference drawn earlier that there may be characteristic differences in the incidence of pausing between lines; it can now be seen that it may have arisen because relatively more non-pausing birds were being included in the under 22-egg class for one line while some were pausing in another without falling below the 22-egg limit. As the same source of confusion may be operating in the interperiod difference which was reported for 1935-39 and 1945-49 (Blyth, 1952), a re-check of all March data for the two lines has been made. There were 15 B and 11 I annual samples considered of sufficient size for examination (19 pullets and over). When the birds with greater than single day gaps were eliminated the difference between the estimate for mean rate of production from this and from the 22-up classification was 0·62 eggs with a standard error of 0·10 for B, and $-0{\cdot}06 \pm 0{\cdot}10$ for I in favour of the latter technique of measurement; this corresponds well with the observations made on the restricted data and confirms the view that rate in the B line had been consistently overestimated.

The situation with regard to changes in the proportion of gaps between the two half decades is demonstrated in table 5. For both lines there is a significant increase in the number of birds with gaps over 4 days between pre- and post-war periods ($Chi^2 = 9$, *df* 1, in each case); when the worst year (1946) is excluded the difference is no longer statistically significant but it is still in the same direction. Two to four day gaps in the B line also behave in the same way, but in I it is in the earlier period that small irregularities are more frequent, and so much so that when the two classifications are added together the two periods are practically alike in their proportions of pausing birds. This discrepancy between the two lines however may be more apparent than real: if there is a tendency towards

greater divergence from the potential maximum rate in more recent times this could occur in high producers as the absence of single interclutch eggs, and would go undetected into the estimate of rate, but in pullets in which the rate of laying was not far from the 50 per cent. level it is manifestly impossible for interruptions to happen without bringing them into the categories classifying pausing birds. Thus a slight shift towards more irregularities in I might not be evident in birds functioning close to their maximum because their high basic rate would hide this weakening of their ability ; it would be mainly the proportion already showing gaps which could measurably express this deterioration. In the B line with its lower average rate, more birds would be near the critical level where any downward trend would be recognisable with the criteria used. On this assumption,

TABLE 5

Percentage of maximum gaps

	B			I		
	No. of birds	2-4 days	Over 4 days	No. of birds	2-4 days	Over 4 days
1935-40* .	305	24	11	143	34	7
1945-49 . .	397	28	20	185	25	19
do. excl. 1946	338	30	14	143	26	13

* 1937 data excluded because there were too few I birds.

among pullets described in table 5, B birds with gaps of four days have increased in number in the more recent period at the expense of those showing two to four day gaps, while their ranks in turn have been more than replenished by a decrease in the number of birds with no classifiable interruptions. In I, the latter transfer is not occurring to a detectable extent.

DISCUSSION

The advantages of separating basic rate of laying from pauses in it for the interpretation of variations in production are again evident here. That heterotic effects in the first crosses studied were restricted to reduction of pausing, and were not detectable in basic rate, is a point of considerable interest which merits further investigation. In particular, the question arises whether it is a phenomenon of general validity for the trait, and occurs in breed crosses which are superior to their parental types, or if it is confined to the field of interline matings where crossing overcomes inbreeding decay.

The earlier idea (Blyth, 1952) that there were differences in the incidence of pausing birds in the inbred lines is not substantiated by

the present analysis ; it now appears to have arisen because the original inference was drawn from data in which the criteria used did not sufficiently differentiate between pullets with a low basic rhythm and those with actual interruptions in production. The weight of evidence however is still in favour of the view that there has been a slight increase in the proportion of pausing birds between the two five-year periods, 1935-39 and 1945-49, accompanying the increase in basic rate found there. This, and the greater ability of the crosses to resist interruptions in laying while not exceeding the better parental line in potential rate, point to the connection between these two components of production being of an indirect nature.

The corollary of such an assumption is that the major, or majority of, deficiencies must be complementary in the two lines, so they provide no evident reason for equality in the degree of pausing. It may be that the effective basis of degeneration takes the form of a multiplicity of small, often non-specific, genetic changes, which while increasing genetic variability, yield a greater uniformity of phenotypic expression in the lines. This would be in accord with the lack of exhaustion of genetic variation found by Lerner and Dempster (1951) in highly selected stocks and discussed by them in relation to genetic homeostasis.

The distinction between fluctuations in basic maximum rate and digressions from it may be purely arbitrary in practice but the facts lead to the conclusion that they have separate fundamental sources. Apart from any importance that this would have in the formulation of selection indexes for the more rapid improvement of flocks (*v.* Lerner, 1950), it might come to be of considerable technical value. In particular it gives hope of some relief from the labour of trap-nesting, for although accurate recording must remain a prerequisite of estimations of basic rate, it is only necessary for a restricted period.

As to pausing, the present study points to the genetic unimportance of the smaller interruptions in laying so that, for comparisons on this basis, less detailed information may prove just as satisfactory as full-time trapping. Reports on the relative reliability of a number of techniques of intermittent and part-time recording are available (Dudley, 1931 ; Norskog, 1948 ; Read, 1949) but concrete suggestions as to which would be best adapted to gaining selective control over this aspect of production must await further investigation. Winter pause, moult, and in some breeds, broodiness, may continue to require separate attention, but differences between birds in respect of the " non-specific " pausing encountered here may be identifiable at certain seasons without recourse to observation of the entire annual cycle. Again, if pausing, as distinct from fluctuations in rate, involves a definite cessation and re-initiation of the ovulatory rhythm, it could probably be identified sufficiently accurately by routine observation of comb condition in small flocks where birds are marked with large numbered visible wing tabs ; in larger commercial projects however

this would probably offer more technical difficulties than procedures like 5-day-week trapnesting or whatever other objective measurement was found to fulfil requirements.

Finally, because of the loss of information which must result from confusing the effects of their variations with those of basic rate when pullet production is evaluated from a single figure, the possibility of measuring pausing of all types from annual records by correcting the latter for rate is also one that might repay serious consideration.

SUMMARY

An analysis of the March production in a small number of replications of an interline cross indicates that its superiority over the parental types rest on two kinds of variations in egg numbers, (*a*) a basic maximum rate or rhythm, and (*b*) gaps constituting divergencies from it. The basic rate manifested equalled, but did not exceed, that of the higher producing line. The proportion of cross birds pausing for more than four days is very small and provides a source of distinction from both inbreds.

A previous deduction that there were differences in the incidence of pausing between inbred lines now appears to have originated in an artifact arising from the criterion of classification used, but re-examination of the data still suggests that the proportion of pausing birds in them has increased in recent years.

It is concluded that the two types of variation distinguished have separate and independent origins. The possible implications of this in regard to practical methods of recording egg production for selection purposes are discussed.

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CHROMOSOME NUMBERS OF *COLEOPTERA* *

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THE present is a complete list of the chromosome numbers of Coleoptera. That in Makino's (1951) *An Atlas of the Chromosome Numbers in Animals* is replete with errors : not in the numbers themselves —almost without exception, these have been faithfully recorded from the originals—but in the spelling of the specific, generic, and family names, as well as in the nomenclature and systematic disposition of many of the species.† Considering the difficulties with which Makino was faced, the coverage of the literature is good, perhaps no more than 14 determinations by nine authors being omitted.

I had earlier intended to compile a list of some 160 chromosome determinations, which I have made as time permitted during the course of the past eight years, together with others that have appeared in print, and to publish them as a supplement bringing those given by Harvey (1916 and 1920) up to date, but it now appears that a complete revision of Makino's list is warranted. It is perhaps noteworthy that 11 families find themselves represented for the first time and that the total of cytologically known Coleoptera now reaches 340. According to Makino's tabulation, this number is surpassed among Insecta only in the Orthoptera and Heteroptera but in no other animal group, and constitutes approximately 10 per cent. of the species of animals whose chromosome numbers have been recorded. The distribution of species, genera, subfamilies, and families by haploid number of autosomes and by sex-chromosome type is given graphically in fig. 1.

In the accompanying tabulation it has been considered advisable to arrange the species not in alphabetical sequence under families (a procedure followed by Makino and by Harvey) but so far as is possible in phylogenetic sequence, since it is only through a logical grouping based on current concepts of taxonomic relationships that the full import of the cytological findings becomes evident. The systematic arrangement adopted herein is that devised by Leng (1920) on the basis of adult morphology, and his catalogue is also taken as

* Contribution No. 48, Division of Forest Biology, Science Service, Department of Agriculture, Ottawa, Canada.

† Thirty-three spelling mistakes occur among the total of 180 determinations tabulated ; 45 species are retained in genera from which they are now, or were even at the time of first publication, removed ; and a few, for example *Silpha perforata*, are listed under the incorrect family. The majority of these errors and all the obsolete names have been carried over from the original authors. It is regrettable that cytologists in general have been, and many still are, remarkably lax in their dealing with taxonomic nomenclature. But unfortunately many purely typographical errors have arisen *de novo* during the printing of both the original Tokyo and the first American editions.

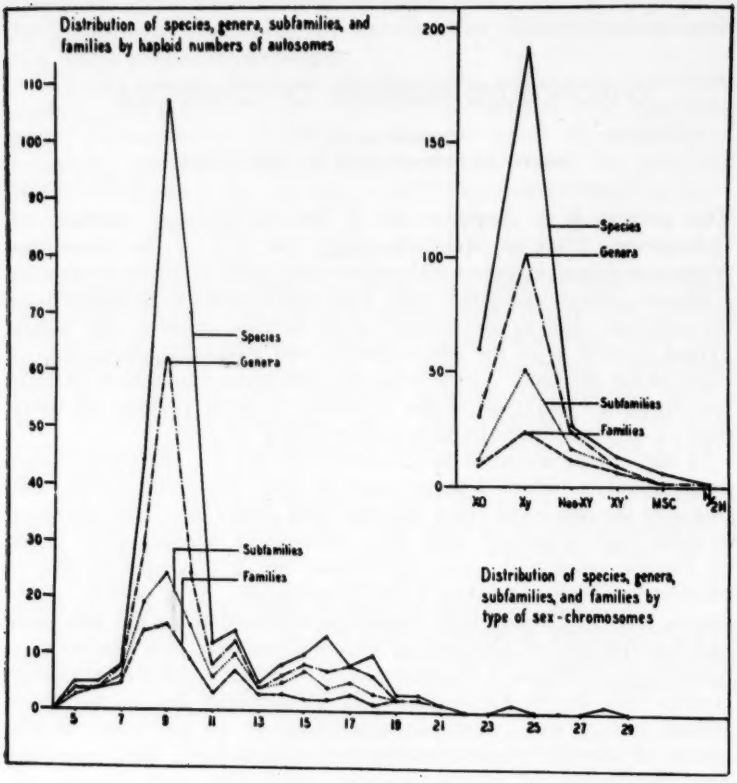
Distribution of species, genera, subfamilies, and families by haploid numbers of autosomes
Species
Genera
Subfamilies
Families
Distribution of species, genera, subfamilies, and families by type of sex-chromosomes
XO
Xy
Neo-XY
'XY'
MSC
2N

FIG. 1.

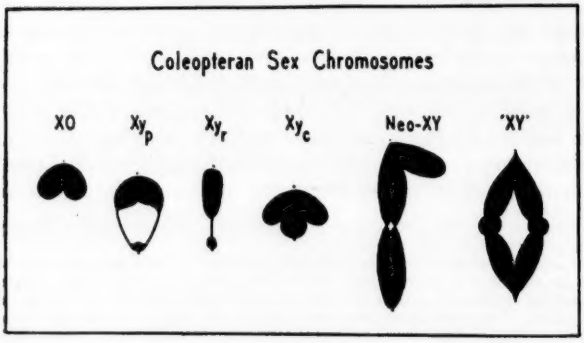
Coleopteran Sex Chromosomes
XO
Xy$_p$
Xy$_r$
Xy$_c$
Neo-XY
'XY'

FIG. 2.

the authority for questions of nomenclature. Whereas Leng and his co-workers were concerned only with Coleoptera of America, north of Mexico, many of the species listed here occur only outside North America; the disposition and nomenclature of such exotic species are those given in the *Coleopterorum Catalogus*.

With but few exceptions all taxonomic determinations of my material were made by W. J. Brown, Systematic Entomology, Science Service; it is a distinct pleasure to record my debt of gratitude to him for these and for guidance in questions of synonymy.

GENERAL NOTES CONCERNING THE LIST

Papers preceding Stevens (1905) are largely in error or open to doubt; they have therefore, with the exception of a determination by Prowazek (see footnote 41), been omitted but are fully listed by Harvey (1916) and Makino (1951). It has not been possible to secure a few of the papers cited by Makino; references to these are placed in parentheses. Unless otherwise stated, undetermined species I have examined originated from the Lake Kipewa region in the Province of Quebec. Components marked with an asterisk are considered as parts of new families by Böving and Craighead (1931).

The first number column gives the somatic chromosomes according to sex, the second gives the number of autosomal pairs and the sex chromosomes.

The following symbols are used: "XY", indistinguishable or unidentified sex chromosomes; x and y, relatively small sex chromosomes; p, r, and c, parachute-, rod-, and centric-associations respectively; neo-XY, derivative, or complex, sex-determining mechanism (see text fig. 2); s, supernumerary chromosome; Parth., Parthenogenetic.

The list has been compiled up to April 1952.

LIST OF CHROMOSOME NUMBERS

I ADEPHAGA[1]: 1. CARABOIDEA

i *CICINDELIDÆ*[2]

CICINDELINI			
Cicindela purpurea	22 ♂	10+Xx	Goldsmith '19
ancocisconensis	22 ♂, 24 ♀	10+Xx : XXxx	,,
repanda	22 ♂	10+Xx	,,
,, Dej.	20 ♂	9+Xy$_c$	Smith '50
tranquebarica[3]	22 ♂	10+Xy$_c$[3]	Stevens '09
	22 ♂, 24 ♀	10+Xx : XXxx	Goldsmith '19
pimeriana[4]	20 ♂	9+Xy$_c$	Stevens '06
sexguttata	22 ♂	10+Xx	Goldsmith '19
s. sexguttata Fab.	22 ♂	...	Smith unpub.
punctulata	22 ♂	10+Xx	Goldsmith '19
scutellaris lecontei Hald.	*ca.* 20 ♂	9+Xy$_c$	Smith unpub.

ii *CARABIDÆ*

CARABINÆ			
Carabus serratus Say	...	12 +Xy	Smith unpub.
HARPALINÆ-BISETOSÆ			
BEMBIDIINI			
Bembidion carinula Chaud.	...	11 +" XY "	"
bifossulatum Lec.[5]	...	11 +" XY "	"
PTEROSTICHINI			
Euferonia coracina Newn.	...	18 +X	"
Pœcilus lucublandus Say	...	17 +neoXY	"
AMARINI			
Celia erratica Sturm	...	15 ?+neoXY	"
Amara impuncticollis Say	...	17 +neoXY	"
AGONINI			
Sericoda obsoleta Say	...	17 +neoXY	"
Agonum sinuatum Dej.[6]	...	12 +neoXY	"
extensicolle Say [6]	...	18 ?+X	"
cupripenne Say [6]	...	17 +neoXY	Smith '50
retractum Lec.[6]	...	18 +X	Smith unpub.
Platynus sp.[7]	37 ♂	18 +X	(Yosida '51)
DRIPTINI			
Galerita bicolor	30 ♂	Xy	Stevens '06
LEBIINI			
Dromius piceus Dej.	25 ♂	12 +X	Smith unpub.
HARPALINÆ-UNISETOSÆ			
CHLÆNIINI			
Chlænius pennsylvanicus [8]	...	9 +Xy [8]	Stevens '06
tricolor Dej.	...	18 +X	Smith unpub.
pallipes	37 ♂	18 +X	(Yosida '51)
æstivus	...	16 +Xy	Stevens '06
laticollis Say	...	18 +X	Smith unpub.
Anomoglossuse marginatus	...	18 +X	Stevens '06
HARPALINI			
Harpalus erythropus Dej.	...	15 +neoXY	Smith unpub.
Agonoderus lecontei Chaud.	...	(12 +X) ?	"
ANTHIINI			
Anthia sexguttata	35 ♂	17 +X	Asana *et al.* '42

iii *DYTISCIDÆ*

COLYMBETINÆ			
Agabus confinis Gyll.	...	20+" XY "	Smith unpub.
Colymbetes fuscus	35-37 ♀	...	Günthert '10
DYTISCINÆ			
Dytiscus marginalis L.	36-41 ♂	...	Henderson '07
	38 ♂	18+" XY "	Schäfer '07
	40 ♀	...	Debaisieux '09
circumcinctus	38 ♂	18+" XY "	Schäfer '07
sp.	38-40 ♀	...	Günthert '10

2. GYRINOIDEA

GYRINIDÆ

Dineutes americanus Say	*ca.* 44 ♂	*ca.* 21_{II}	Smith unpub.
horni Rbts.	...	*ca.* 21_{II}	"

II POLYPHAGA: 1. HYDROPHILOIDEA

HYDROPHILIDÆ

Hydrous acuminatus	30 ♂	14+Xy_r	Asana *et al.* '42
piceus [9]	30 ♂	15_{II}	Arnold '08
triangularis Say	30 ♂	14+Xy_p	Smith unpub.
Tropisternus lateralis Fab.	...	8+Xy_p	,,

2. SILPHOIDEA

SILPHIDÆ

Necrophorus sayi	13 ♂	6+X	Stevens '09
vespilloides Hbst.	13 ♂	6+X	Smith '50
Silpha surinamensis Fab.	...	*ca.* 12+Xy_p	Smith unpub.
noveboracensis Forst.	26 ♂	12+Xy_r	,,
americana	40 ♂	19+Xy	Stevens '06
perforata [10]	...	19+X	(Yosida '51)

3. STAPHYLINOIDEA

STAPHYLINIDÆ

STAPHYLININÆ			
XANTHOLININI			
Nudobius cephalus Say	...	13+Xy_p	Smith '50
STAPHYLININI			
Staphylinus violaceus	...	21+Xy	Stevens '09
Philonthus politus L.	...	*ca.* 19+Xy_r	Smith unpub.
Ontholestes cingulatus [11]	26 ♂	12+Xy	Stevens '09
,, ,, Grav.	...	12+Xy_p	Smith unpub.
Creophilus maxillosus villosus Grav.	...	*ca.* 17+Xy	,,
ALEOCHARINÆ			
Aleochara sp.	...	8+neoXY	,,
Unknown [12]			
"Rove beetle"	28 ♂	14_{II}	Stevens '09

4. CANTHAROIDEA

i *LAMPYRIDÆ* [13]

LUCIDOTINI			
Lucidota californica Mots.	...	9+X	Smith and Maxwell '53
corrusca [14]	19 ♂	...	Stevens '06, '09
,, L.	19 ♂, 20 ♀	9+X	Smith and Maxwell '53
sp., nr. *corrusca* L.	...	9+X	,,
PHOTININI			
Pyractomena angulata Say	...	9+X	,,
		9+X+0–4[s]	,,
borealis Rand.	...	9+X	,,
Photinus consanguineus [15]	19 ♂, 20 ♀	9+X	Stevens '09
sp.	...	9+X	Smith and Maxwell '53
PHOTURINI			
Photuris pennsylvanica [16]	19 ♂, 20 ♀	9+X	Stevens '09
pennsylvanica complex	...	9+X	Smith and Maxwell '53

ii *CLERIDÆ*

Thanasimus dubius Fab.	...	8+Xy$_p$	Smith '50
Clerus nigripes rufiventris Spin.	18 ♂	8+Xy$_p$	Smith unpub.
Trichodes nutalli Kby.	...	8+Xy$_p$	,,

5. LYMEXYLOIDEA

MICROMALTHIDÆ[17]

Micromalthus debilis Lec.	10 ♂, 20 ♀	10$_i$	Scott '36

6. MORDELLOIDEA

i *CEPHALOIDÆ*

Cephaloon lepturides Newn.	...	8+Xy$_p$	Smith unpub.

ii *MELOIDÆ*[18]

MELOINÆ			
Mylabris pustulata[19]	22 ♂	10+Xy$_r$	Asana *et al.* '42
Melæ sp.	20 ♂	9+Xy$_r$	,,
LYTTINÆ			
Epicauta cinerea	20 ♂	9+Xy	Stevens '09
pennsylvanica	20 ♂	9+Xy	,,
murina Lec.	...	9+Xy$_p$	Smith unpub.

7. ELATEROIDEA

i *ELATERIDÆ*

PYROPHORINÆ			
PYROPHORINI			
Adelocera rectangularis Say	17 ♂	8+X	Smith unpub.
LEPTUROIDINI			
Limonius griseus[20]	17 ♂	8+X	Stevens '09[20]
æger Lec.	20 ♂	9+Xy$_p$	Smith '50
Ctenicera ochreipennis Lec.[21]	...	10+Xy$_p$	Smith unpub.
.....			
hieroglyphica Say	...	10+X	,,
propola propola Lec.	21 ♂	10+X	,,
.....			
appressa Rand.	...	10+Xy$_p$	,,
.....			
mediana Germ.	...	10+Xy$_p$	,,
.....			
splendens Zieg.	19 ♂	9+X	,,
æripennis æripennis Kby.	19 ♂	9+X	,,
a. destructor Brown	19 ♂	9+X	,,
appropinquans Rand.	19 ♂	9+X	,,
semimetallica Wlk.	...	9+X	,,
.....			
nitidula Lec.	...	8+X	,,
rufopleuralis Fall	...	8+X	,,
arata Lec.	...	8+X	,,
.....			
inflata Say	...	9+Xy$_p$	,,
Eanus maculipennis Lec.	...	9+Xy$_p$	,,
estriatus Lec.	...	9+Xy$_p$	,,

ELATERINÆ			
AGRIOTINI			
Agriotella bigeminata Rand.	...	9+X	Smith unpub.
ELATERINI			
Ampedus apicatus Say	19 ♂	9+X	,,
melsheimeri Leng	...	9+X	,,
deletus Lec. (?)	...	9+X	,,
sp., nr. *deletus* Lec.	...	9+X	,,
,,	...	10+X	,,
sp., nr. *miniipennis* Lec.	...	9+X	,,
fusculus Lec.	...	9+X	,,
luctuosus Lec.	...	9+X	,,
" Elater sp. I "	19 ♂, 20 ♀	9+X	Stevens '06
" Elater sp. II "	19 ♂	9+X	,,
MELANOTINI			
Melanotus castanipes Payk.	18 ♂	...	Smith unpub.
leonardi Lec.	...	9+X	,,
sp., nr. *communis* Gyll.	19 ♂	9+X	,,
sp.	18 ♂	...	,,
trapezoideus Lec. (?)	19 ♂	9+X	,,
CARDIOPHORINÆ			
Cardiophorus fenestratus Lec.	22 ♂	10+Xy_p	,,
gagates Er.	...	10+Xy_p	,,
togatus Horn	...	10+Xy_p	,,
convexulus Lec.	...	10+Xy_p	,,

ii *BUPRESTIDÆ*

JULODINI			
Julodis whithilli	24 ♂	11+neoXY [22]	Asana *et al.* '42
Sternocera nitidicollis [23]	26 ♂	12+neoXY [22]	,,
lævigata	26 ♂	12+neoXY [22]	,,
CHALCOPHORINI			
Chalcophora lacustris Lec.	21 ♂, 22 ♀	10+X	Smith unpub.
Euchroma gigantea	...	12+Xy	Nichols '10
BUPRESTINI			
Dicerca prolongata Lec.	20 ♂	9+Xy_p	Smith unpub.
tenebrosa Kby.	20 ♂	9+Xy_p	,,
Buprestis fasciata Fab.	20 ♀	...	,,
Melanophila drummondi Kby.	16 ♂	Xy	,,
acuminata DeG.	...	5+Xy_p	,,
CHRYSOBOTHRINI			
Chrysobothris dentipes Germ.	16 ♂	7+Xy_p	,,
AGRILINI			
Agrilus anxius Gory	22 ♂, 22 ♀	10+Xy_p : XX	Smith '49
liragus Barter and Brown	20 ♂, 20 ♀	9+neoXY : XX	,,
sp., nr. *pensus* Horn	...	Xy_p	Smith unpub.
politus pseudocoryli Fish.	...	9+" XY "	,,
sp.	...	9+neoXY	,,
Unknown			
" Spruce borer sp. I "	...	9+Xy	Stevens '06
" Spruce borer sp. II "	...	10+Xy	,,

8. BYRRHOIDEA

i *DERMESTIDÆ*

DERMESTINI			
Dermestes talpinus Mann.	...	8+Xy_p	Smith unpub.
lardarius L.	...	8+Xy_p	,,
signatus Lec.	18 ♂	8+Xy_p	,,
ANTHRENINI			
Anthrenus sp.	...	8+Xy_p	Smith '50

ii *BYRRHIDÆ*

Cytilus alternatus Say	18 ♂	Xy	Smith unpub.

9. CUCUJOIDEA

i *NITIDULIDÆ*

Nitidula bipunctata L.	...	9+Xy_p	Smith '50
rufipes L.	...	9+Xy_p	Smith unpub.

ii *CUCUJIDÆ*

Oryzæphilus surinamensis	13-14 ♂	" 7 elements "	McMullen '28

iii *EROTYLIDÆ*

Triplax thoracica Say	...	8+neoXY	Smith unpub.

iv *COCCINELLIDÆ*

COCCINELLINÆ			
HYPERASPINI			
Brachyacantha ursina Fab.	...	7+neoXY	Smith unpub.
SYNONYCHINI			
Synonycha grandis Thunb.	20 ♂	9+Xy_r	Yosida '44, '46
Cælophora inæqualis [24]	20 ♂	9+Xy_r	(Yosida '49, '51)
Aiolocaria mirabilis [25]	17 ♂	8+X	(T. and Y. '37)
	20 ♀	...	(Yosida '49, '51)
COCCINELLINI			
Coleomegilla maculata lengi Timb.	20 ♂	9+Xy_p	Smith unpub.
Hippodamia tredecimpunctata L.	20 ♀	...	Yosida '44
t. tibialis Say	20 ♂	9+Xy_p	Smith '50
Coccinella trifasciata L.	...	9+Xy_p	Smith unpub.
transversoguttata Fald.	...	9+Xy_p	,,
bruchii [26]	...	9+" XY "	(T. and Y. '37)
,, Muls.[26]	18 ♂	8+Xy_r	Yosida, '44
crotchi Lewis	20 ♂	9+Xy_r	,,
axiridis Pallas [27]	16 ♂	7+Xy_p	Li '40
		7+Xy_r	Yosida, 44
Adalia bipunctata	20 ♂	9+Xy	Stevens '06
,, ,, L.	...	9+Xy_p	Smith unpub.
Cleis hudsonica Csy.	12 ♂	5+" XY "	,,
	...	5+" XY "+2s	,,
Anisocalvia duodecim-maculata Gebl.	...	9+Xy_p	,,
quatuordecimguttata L.	20 ♂	9+Xy_p	,,
,, ,, L.[28]	...	9+Xy_r	Yosida '44
Propylæa japonica	...	9+Xy	(Yosida '49, '51)
Anatis mali auct.	18 ♂	8+neoXY	Smith unpub.

EPILACHNINÆ			
Epilachna borealis	18 ♂	8+Xy	Stevens '06
	18 ♂, 18 ♀	...	Hoy '18
nipponica Lewis [29]	20 ♂	9+Xy_r	Yosida '44
vigintioctomaculata	...	8+" XY "	(T. and Y. '37)
,, Mots.[30]	20 ♂	Xy	Yosida '48
vigintioctopunctata Fab.	18 ♂ [31]	Xy	,,
pustulosa Kôno [32]	20 ♂	Xy	,,
chrysomelina F. × *capensis* Thunb.	18 ♂	...	Strasburger '36
Unknown			
Various undetermined species	20 ♂	9+Xy	Stevens '09
10. TENEBRIONOIDEA			
i *ALLECULIDÆ*			
Isomira quadristriata Couper	20 ♂	9+Xy_p	Smith '50, '52*b*
ii *TENEBRIONIDÆ*			
ERODIINÆ			
Erodius nitidicollis Sol.	20 ♂	9+Xy_r	Guénin '51*b*
edmondi Sol.	20 ♂	9+Xy_r	,,
Leptonychus curvicornis Peyer.	20 ♂	9+Xy_r	,,
TENTYRIINÆ			
Tentyria mucronata Stev.	20 ♂	9+Xy_r	Guénin '50
subcosta Sol.	20 ♂	9+Xy_r	Guénin '51*a*
Mesostema angustata præsahariana Koch.	20 ♂	9+Xy_r	,,
Genus nr. *Hylocrinus* Csy. (Texas)	20 ♂	9+Xy_p	Smith '52*b*
Zopherus haldemani Sallé [33]	16 ♂	7+Xy	Smith '52*b*, '53
ELENOPHORINÆ			
Elenophorus collaris L.	26 ♂	12+Xy_r	Guénin '50
AKIDINÆ			
Akis bacarozzo Schrank	16 ♂	7+neoXY	,,
PIMELIINÆ			
Pimelia bipunctata Fab.	18 ♂	8+Xy_r	,,
servilei Sol.	18 ♂	8+Xy_r	Guénin '51*a*
aranacea Sol.	18 ♂	8+Xy_r	,,
grandis latesti Sen.	18 ♂	8+Xy_r	,,
angulata lestei Peyer	18 ♂	8+Xy_r	,,
subquadrata valdani Guer.	18 ♂	8+Xy_r	,,
Ocnera hispida Forsk	18 ♂	8+Xy_r	,,
Prionotheca coronata Ol.	18 ♂	8+Xy_r	,,
BLAPTINÆ			
Blaps waltli Seidl.[34]	34 ♂	15+3 XY	Nonidez '15
lusitanica Hbst.	35 ♂	15+4 XY	Nonidez '14, '20
	19 ♂, 20 ♀	8+2 XY : 4 X	Guénin '49
gigas L.	35 ♂, 38 ♀	15+4 XY : 8 X [35]	,,
mucronata Latr.	36 ♂, 38 ♀	16+3 XY : 6 X [35]	,,
mortisaga L.	36 ♂, 38 ♀ [36]	16+3 XY : 6 X	,,
lethifera Marsh.	37 ♂, 38 ♀	17+2 XY : 4 X	,,
PEDININÆ			
Opatrinus aciculatus Lec.	20 ♂	9+Xy_p	Smith '52*b*
DIAPERINÆ			
Diaperis boleti L.	14 ♂	6+neoXY	Guénin '50

ULOMINÆ			
Tribolium castaneum Hbst.	20 ♂, 20 ♀	9+Xy_p : XX	Smith '52*a*, *b*
confusum Duval	18 ♂, 18 ♀	8+neoXY : XX	,,
destructor Uyttenb.	18 ♂, 18 ♀	8+neoXY : XX	,,
TENEBRIONINÆ			
Alobates pennsylvanica DeG.	20 ♂	9+Xy_p	Smith '52*b*
Scotobates calceratus Fab.	...	8+neoXY	,,
Upis ceramboides L.	20 ♂	9+Xy_p	,,
Tenebrio obscurus Fab.	20 ♂	9+Xy_r	Guénin '50
molitor	20 ♂, 20 ♀	9+Xy	Stevens '05[36]
,, L.	20 ♂	9+Xy_r	Guénin '50
		9+Xy_p	Smith '50, '51, '52*b*
picipes Hbst.	20 ♂	9+Xy_p	Smith '52*b*

iii *LAGRIIDÆ*

Arthromacra ænea Say	14 ♂	6+neoXY	Smith '50, '52*b*

iv *MELANDRYIDÆ*

*PENTHINI			
Penthe obliquata	16 ♂	7+Xy	Stevens '09
,, ,, Fab.	...	7+neoXY	Smith '52*b*
MELANDRYINI			
Serropalpus substriatus Hald.	20 ♂	9+Xy_p	Smith '50, '52*b*
Dircæa quadrimaculata Say	...	9+Xy_p	Smith '52*b*

II. SCARABÆOIDEA

i *SCARABÆIDÆ*

COPRINÆ			
Phanæus vindex MacL.[37]	12 ♂	5+" XY "	Hayden '25
igneus MacL.	12 ♂	5+" XY "	,,
APHODIINÆ			
APHODIINI			
Aphodius fimetarius L.	...	9+Xy_p	Smith unpub.
EUPARIINI			
Atænius spretulus Hald.	*ca.* 20 ♂	...	,,
*GEOTRUPINÆ			
Geotrupes balyi Jek.	22 ♂	Xy	,,
MELOLONTHINÆ			
SERICINI			
Serica tristis Lec.	20 ♂	9+Xy_p	Smith '50
MELOLONTHINI			
Diplotaxis sp. (Texas)	20 ♂	9+Xy_p	Smith unpub.
Phyllophaga gracilis [38]	20 ♂, 20 ♀	9+Xy	Shaffer '20
fusca [38]	20 ♂, 20 ♀	9+Xy	,,
delata [38]	20 ♂, 20 ♀	9+Xy	,,
sp., *crenulata* group	*ca.* 20 ♀	...	Smith unpub.
tristis [38]	20 ♂, 20 ♀	9+Xy	Shaffer '20
RUTELINÆ			
ANOMALINI			
Popillia japonica Newn.[39]	18 ♂	8+Xy	Yosida '49*b*
Anomala corpulenta Mots.	18 ♂	8+Xy	,,
rufocuprea Mots.	18 ♂	8+Xy	,,

RUTELINI			
Pelidnota punctata [40]	20 ♂, 20 ♀	9+Xy	Shaffer '20
Cotalpa lanigera	20 ♂, 20 ♀	9+Xy	,,
DYNASTINÆ			
Oryctes nasicornis L.[41]	12 ♂	5+"XY"	Prowazek '02
CETONIINÆ			
CETONIINI			
Euphoria inda	20 ♂	9+Xy	Stevens '06
,, ,, L.	...	9+Xy$_p$	Smith unpub.
Glycyphana fulvistemma Mots.	20 ♂	9+Xy	Yosida '49*b*
TRICHIINI			
Trichiotinus assimilis Kby.	...	9+Xy$_p$	Smith unpub.
Trichius fasciatus L.	20 ♂	9+Xy	Yosida '49*b*

ii *LUCANIDÆ*

Psalidoremus inclinatus [42]	19 ♂	9+X	(T. and Y. '37)

iii *PASSALIDÆ*

Popilius disjunctus [43]	26 ♂, 26 ♀	12+Xy	Shaffer '17
,, ,, Ill.	26 ♂	12+neoXY	Smith unpub.

12. CERAMBYCOIDEA

i *CERAMBYCIDÆ*

CERAMBYCINÆ			
ELAPHIDIONINI			
Elaphidion, prob. *parallelus* Newn.	...	9+Xy$_p$	Smith unpub.
LEPTURINI			
Acmæops proteus Kby.	...	10+Xy$_p$	,,
CLYTINI			
Cyllene robiniæ [44]	...	9+Xy	Stevens '09
LAMIINÆ			
MONOCHAMINI			
Monochamus notatus Drury	...	9+Xy$_p$	Smith '50
scutellatus Say	...	9+Xy$_p$	Smith unpub.
marmorator Kby.	...	9+Xy$_p$	,,
NIPHORINI			
Pterolophia caudata	20 ♂	9+Xy	(Yosida '51)
GRAPHISURINI			
Graphisurus obsoletus Oliv.	...	9+Xy$_p$	Smith unpub.
PHYTŒCIINI			
Oberea tripunctata [45]	...	Xy	Stevens '09
,, ,, Swed.	...	9+Xy$_p$	Smith unpub.
mandarina Fab.	...	9+Xy$_p$	,,
affinis Leng	...	9+Xy$_p$	,,
TETRAOPINI			
Tetraopes tetrophthalmus [46]	20 ♂	9+Xy	Stevens '09
,, ,,	20 ♂	9+XY [47]	Snyder '34
,, Forst.	...	9+Xy$_p$	Smith unpub.
femoratus	20 ♂	9+XY [47]	Snyder '34

ii *CHRYSOMELIDÆ*

*DONACIINÆ			
Donacia hirticollis Kby.	...	13+Xy$_p$	Smith unpub.
subtilis Kunze	...	13+Xy$_p$	,,
*CRIOCERINÆ			
Lema trilineata	32 ♂	15+Xy	Stevens '09
,, ,, auct.	...	15+Xy$_p$	Smith unpub.
CRYPTOCEPHALINÆ			
Cryptocephalus venustus Fab.	*ca.* 22 ♂	*ca.* 12$_{II}$	,,
*EUMOLPINÆ			
Chrysochus auratus	...	12+Xy$_r$	Stevens '09
,, ,, Fab.	...	12+Xy$_c$	Smith unpub.
*CHRYSOMELINÆ			
CHRYSOMELINI			
Labidomera clivicollis [48]	...	16+Xy	Stevens '09
Leptinotarsa signaticollis [49]	33-34 ♂, 36 ♀	16+XX : 4 X	Wieman '10
decemlineata [50]	36 ♂	17+Xy	Stevens '06
,, Stål.	35 ♂, 36 ♀	17+X : XX	Guénin and Scherler '52
,, Say	...	17+X	Smith unpub.
Calligrapha similis [51]	...	11+X	Stevens '09
philadelphica L.	...	11+X	Smith unpub.
multipunctata bigsbyana Kby.	...	11+Xy$_p$	,,
Chrysolina exanthematica Wied.[51]	23 ♂	11+X	Yosida '44
Chrysomela interrupta auct. in part	34 ♂	16+Xy$_p$	Smith unpub.
sp.	34 ? ♂	16+Xy$_p$	,,
lapponica [52]	...	16+Xy	Stevens '09
tremulæ auct.	...	16+Xy$_p$	Smith unpub.
Melasoma æneа [53]	...	16+Xy	(Yosida '51)
populi [53]	32 ♂	15+Xy$_r$	,,
PHYLLODECTINI			
Phytodecta americana Schffr.	24 ♂	Xy	Smith unpub.
variabilis	24 ♂	11+Xy	Galán '31
*GALERUCINÆ			
ATYSINI			
Trirhabda virgata	28 ♂, 28 ♀	13+Xy	Stevens '06
canadensis	30 ♂, 30 ♀	14+Xy	,,
,, Kby.	30 ♂	14+Xy$_p$	Smith unpub.
Galerucella vaccinii Fall	...	16+Xy$_p$	,,
cavicollis Lec.	...	16+Xy$_p$	,,
nymphææ L.	...	16+Xy$_p$	,,
OIDINI			
Rhaphidopalpa femoralis [54]	...	28+Xy	(Yosida '49, '51)
DIABROTICINI			
Diabrotica duodecimpunctata [55]	19, 20 ♂	9+X+o−4s	Stevens '08
soror [56]	19-21 ♂	9+X+o−4s	,,
Acalymma vittata [57]	21 ♂	10+X	,,
	21 ♂, 22 ♀	10+XX	Hoy '14, '18
LUPERINI			
Luperus discrepans Baly	...	15+neoXY	Yosida '44
Luperodes præustus Mots.[58]	32 ♂, 32 ♀	15+neoXY	,, '49*a*
AGELASTICINI			
Agelastica cærulea Mots.[59]	24 ♂	11+Xy$_r$	,, '44

HALTICINÆ			
BLEPHARIDINI			
Blepharida rhois . . .	...	15+Xyp	Stevens '06
HALTICINI			
Haltica subplicata Lec. .	23 ♂	11+X	Smith unpub.
chalybea . . .	22 ♂	10+X+y [60]	Stevens '09
Argopus punctipennis [61] . .	...	24+Xy	(Yosida '49, '51)
*HISPINÆ			
Anoplitis inæqualis auct.[62] .	...	8+Xyp	Smith '50
Chalepus dorsalis [62] . .	16 ♂	7+Xyp	Stevens '06
*CASSIDINÆ			
Chelymorpha cassidea [63] .	22 ♂, 22 ♀	10+Xyp	,,
Deloyala guttata [64] . .	18 ♂	8+Xy	Nowlin '06
Plagiometriona clavata [64] .	18 ♂	Xy	Stevens '09
Agroiconota aurichalcea [64] .	22 ♂	10+Xy	Nowlin '06
iii *BRUCHIDÆ*			
AMBLYCERINÆ			
Zabrotes subfasciatus Boh. .	26 ♂, 26, 27 ♀	12+X+y : XX+s	Minouchi '35
BRUCHINÆ			
Callosobruchus maculatus [65] .	19 ♂, 20 ♀	9+X	Brauer '28
Acanthoscelides obtectus Say [66]	20 ♀	9+" XY "	Bushnell '36
13. CURCULIONOIDEA			
i *PLATYSTOMIDÆ*			
Euparius marmoreus Oliv. .	...	10+Xyp	Smith '52*c*
ii *CURCULIONIDÆ*			
OTIORHYNCHINÆ			
POLYDRUSINI			
Polydrusus pilosus Gredl.[67] .	...	10+Xy	Suomalainen '40*a*, *b*
undatus F.[68] . . .	...	10+XX	Suomalainen '40*a*
mollis Ström. . . .	22 ♀	22_I Parth.	Suomalainen '40*a*, *b*
SCIAPHILINI			
Sciaphilus asperatus Bonsd. .	33 ♀	33_I Parth.	,,
THYLACITINI			
Strophosomus capitatus DeG.[69]	*ca.* 20 ♂, 22 ♀	10+X : XX	,,
melanogrammus Först. .	34 ♀	31-35_I Parth.	,,
BARYNOTINI			
Barynotus mœrens F. . .	...	55_I Parth.	Suomalainen '47
obscurus F. . . .	...	44_I Parth.	Suomalainen '40*a*, *b*
BRACHYRHININI			
Brachyrhinus geniculatus Germ.[70]	...	10+Xy : XX	Suomalainen '47
inflatus Gyll. . . .	...	10+Xy	,,
i. salebrosus Boh. . .	...	10+Xy	Mikulska '49
arcticus O.F. . . .	22 ♂	10+Xy : XX	Suomalainen '40*a*, '45

armadillo Rossi	...	10+Xy : XX	Suomalainen '47
bisulcatus F.	...	10+Xy : XX	,,
fuscipes Oliv.[71]	22 ♂	10+Xy	,,
	...	10+Xy	Mikulska '49
morio F.	...	10+Xy$_p$: XX	Suomalainen '47
		10+Xy	Mikulska '49
multipunctatus F.[72]	...	10+Xy	,,
niger F.	...	10+Xy : XX	Suomalainen '47
		10+Xy	Mikulska '49
		33$_I$ Parth.	Suomalainen '47
dubius Ström.[73]	...	44$_I$ Parth.	Suomalainen '40*a*, *b*, '45
repletus Boh.	...	10+Xy	Mikulska '49
scaber L.	33 ♀	33$_I$ Parth.	Suomalainen '45, '47
	44 ♀	42-44$_I$ Parth.	Suomalainen '40*a*, *b*, '45, '47
sensitivus Scop.	...	10+Xy$_p$: XX	Suomalainen '47
austriacus F.	...	10+XX	,,
corvus Boh.	...	10+Xy	Mikulska '49
equestris Richt.	...	10+Xy	Suomalainen '47, Mikulska '49
gemmatus Scop.	...	10+Xy : XX	Suomalainen '47
		33$_I$ Parth.	,,
kollari Gyll.	...	10+Xy	Mikulska '49
obsidianus Boh.	...	10+Xy	,,
obtusus Boh.[74]	...	10+Xy	,,
pupillatus Gyll.	...	44$_I$ Parth.	Suomalainen '47
salicis Ström.	...	10+Xy$_p$: XX	,,
		32$_I$ Parth.	,,
singularis L.	...	33$_I$ Parth.	,,
sulcatus F.	...	34$_I$ Parth.	,,
		33$_I$ Parth.	Seiler '47
ligustici L.	*ca.* 30 ♀	33-35$_I$ Parth.	Suomalainen '40*a*, *b*, '45
ovatus L.	33 ♀	30-34$_I$ Parth.	,,
chrysops Hbst.	...	10+XX	Suomalainen '47
TRACHYPHLŒINI			
Trachyphlœus bifoveolatus Beck.	...	32-33$_I$ Parth.	Suomalainen '40*a*, *b*
EPISOMINI			
Episomus turritus[75]	...	9$_{II}$	(T. and Y. '37)
CURCULIONINÆ			
SITONINI			
Sitona lepidus Gyll.[76]	...	10+Xy$_p$	Smith '50, '52*c*
cylindricollis Fåhr.	...	10+Xy$_p$	Smith '52*c*
HYPERINI			
Hypera punctata	...	Xy	Stevens '09
HYLOBIINI			
Hylobius abietis L.	...	10+X	Suomalainen '40*a*, *b*
congener D.S. and M.	22 ♂	10+Xy$_p$	Smith '52*c*
CURCULIONINI			
Curculio obtusus Blanch.	22 ♂	...	Smith unpub.

ANTHONOMINI			
Anthonomus scutellatus Gyll.	...	13+Xy$_p$	Smith '52*c*
*CALENDRINÆ			
Sitophilus granarius L.[77]	12 ♀	5+" XX "	Inkmann '33
" "	24 ♂, 24 ♀	11+Xy$_p$	Smith '52*c*
oryzæ L.[77]	12 ♀	5+" XX "	Tiegs and Murray '38
	11 ♂, 12 ♀	5+X : XX	Gunson '45
"	22 ♂, 22 ♀	10+neoXY : XX	Smith '52*c*

SCOLYTOIDEA

SCOLYTIDÆ

HYLESININÆ			
Dendroctonus engelmanni Hopk.	...	14+Xy$_p$	Smith '52*c*
Hylurgops pinifex Fitch	...	14+Xy$_p$	"
IPINÆ			
Ips pini Say	...	14+Xy$_p$	"

Footnotes.—Quotations are from the original papers unless otherwise stated :

[1] Böving and Craighead (1931) regard this suborder as being logically considered most recent. [2] " Cicindellidæ " in Makino (1951). [3] " *vulgaris* " ; not X_1X_2-Y♂, *contra* Makino (1951). [4] " *primeriana* ". [5] Collected from the north shore of Lake Michigan, although it would not be expected east of Manitoba and Nebraska. [6] *Platynus sens* Leng. [7] " *Palatinus* " in Makino (1951). [8] " *Chalenius* " in Makino (1951) ; probably an incorrect determination (Smith, 1950). [9] Formerly placed in *Hydrophilus*. [10] Not in Carabidæ, *contra* Makino (1951). [11] " *Listotrophus cingulatus* ". [12] Not necessarily genus *Staphylinus* (*v.* Makino, 1951). [13] All species listed have post-reductional division of the X-chromosome ; not Cantharidæ, *contra* Makino (1951). [14] " *Ellychnia* ". [15] " *cansanguineus* " (Makino, 1951). [16] " *Photinus pennsylvanicus* ". [17] Böving and Craighead (1931), with other authors, consider this to be in a third, and most primitive, suborder, the Archostemata. The species listed has haploid parthenogenetic males. [18] *E. permogloanica* is not given in Stevens (1909), *contra* Makino (1951). [19] " *Mylabiris* " (Makino, 1951). [20] " *Limoneus* " = " *Linoneus* " (Makino, 1951) ; not Stevens, '06, *contra* Makino (1951). [21] Species complexes in the genus *Ctenicera* separated according to Brown's arrangement as given in the supplements to Leng (1920). [22] " XO ; X attached to an autosome ". [23] " *S. nitidicolis* ". [24] " *Cælophola* " (Makino, 1951). [25] " *Ithone* ". [26] " *bruckii* " (Makino, 1951). [27] " *Harmonia axyridis* ". [28] " *Calvia 14-guttata* L." [29] " *niponica* ". [30] " = *nipponica* " (Makino, 1951). [31] *Contra* Makino (1951). [32] " *pustlosa* ". [33] Species has pre-metaphase stretch of autosomes and precession of sex chromosomes. [34] " *walthi* " of many cytologists, including Makino (1951). [35] *Contra* Makino (1951). [36] Not Stevens '06, *contra* Makino (1951). [37] " *carnifex* (L.) ". [38] " *Lachnosterna* ". [39] " *Poppilia* " (Makino, 1951). [40] " *Pelidonata* " (Makino, 1951). [41] Compare this complement with those of *Phanæus* spp. [42] " *Paslidoremus* " (Makino, 1951). [43] syn. *Passalus cornutus* Fab. [44] " *Cylene robinia* ". [45] " *Obera* ". [46] " *tetraophthalmus* ". [47] Sex chromosomes as identified by Snyder are incorrect for the former species and, therefore, possibly for the latter. [48] " *Doryphora clivicolis* ". [49] " *signaticolis* " in Makino (1951). [50] " *Doryphora* ". [51] " *Chrysomela* ". [52] " *Lina laponica* ". [53] = *Chrysomela* L. [54] " *Rhaphidopolpa* " in Makino (1951). [55] This, the eastern subspecies, is *D. undecimpunctata howardi* Barber. [56] This, the western subspecies, is *D. u. undecimpunctata* Mann. [57] Formerly placed in *Diabrotica*. [58] = *Luperus* auct. = " *Luperoides* " (Makino, 1951). [59] " *cærulea* ". [60] It is not improbable that this is an XO species, the " y " not associating with the X because it is a supernumerary chromosome. The generic name is alternatively *Altica*. [61] " *A. orientalis* ". [62] Formerly placed in *Odontota* Chev. [63] syn. *C. argus* Licht. [64] " *Coptocycla* ". [65] " *Bruchus quadrimaculatus* ". [66] Not in Curculionidæ, *contra* Makino (1951). [67] Suomalainen uses the European variant *Polydrosus*. [68] syn. *tereticollis* DeG. [69] syn. *Strophosomus rufipes capitatus* DeG. = *Strophosmus* in Makino (1951). [70] American authors refer to the genus as *Brachyrhinus*, Europeans use *Otiorhynchus* (= " *Otiorrhynchus* "). [71] A variety of *clavipes* Bonsd. [72] syn. *irritans* Hbst. [73] syn. *nodosus* O. Müll. [74] syn. *graniventris* Mill. [75] " *turitus* ". [76] = *flavescens* Marsh. nec. F. [77] syn. *Calandra*.

SUMMARY AND ABSTRACT

Approximately 340 species and subspecies of Coleoptera are listed of which about one-half are determinations made by the author. The number of component genera totals 179, the number of families 33. The commonest sex-determining mechanisms are Xy, neo-XY, and XO as follows :—

Xy :	193	species in	112	genera in	24 families
neo-XY :	29	„	24	„	12 „
XO :	60	„	30	„	9 „

The distribution of species, genera, subfamilies, and families by haploid number of autosomes and by sex-chromosome type is given graphically. Parthenogenesis occurs in two families ; compound sex chromosomes are found in a third and possibly a fourth.

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ADDENDUM

Since this list was compiled, reprints of three papers have been received: Virkki (*Ann. Zool. Soc. Zool. Bot. Fenn.* "*Vanamo*", *14*, 1-104, 1951) provides information on 30 additional species in the Scarabæidæ and new determinations for *Trichius fasciatus* L. (2n=19, *contra* Yosida herein) and *Oryctes nasicornis* L. (2n=18 *contra* Prowazek, *v.* footnote 42 herein); Guénin (*Rev. suisse Zool.*, *59*, 277-282, 1952) reports that four European species of *Cicindela* have XXXY : XXX/XXX sex-determining mechanisms; and Yosida (*Papers Co-ord. Comm. Res. Genet.*, *3*, 41-49, 1952) gives determinations for another carabid and another chrysomelid, besides giving *Silpha perforata* Gebler as 2n=20 and 21 (*contra* Yosida, 1951, *v.* Makino, 1951).

CHROMOSOME BEHAVIOUR IN SPECIES HYBRIDS WITH *TRITICUM TIMOPHEEVI*

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INTRODUCTION

THE 28 chromosome wheat species *Triticum timopheevi* has attracted interest on account of its reported cytological behaviour and its application to the genome concept. Lilienfeld and Kihara (1934) had examined the F_1 hybrids between tetraploid wheat species. They had found that the hybrids involving *timopheevi* differed from the rest, were normally sterile, and had poor chromosome pairing. On the basis of chromosome pairing in hybrids they designate the chromosome sets of *timopheevi* by the formula AG in contrast to the AB formula given to the chromosome sets of the other tetraploid species. In their classification of the genus *Triticum*, the species *timopheevi* is also placed in a section of its own thus suggesting a different origin. This suggestion is followed by Sears (1948). Kostoff (1937) obtained similar results to those of Lilienfeld and Kihara, but he interprets them as showing " partial homology " (as measured by metaphase chromosome pairing in hybrids) between the chromosome sets of *timopheevi* and of the other tetraploid species. Kostoff therefore suggests for *timopheevi* the formula Aβ.

In view of this reported behaviour of *timopheevi*, it was decided to investigate hybrids with this species using both F_1's and a range of colchicine derived amphiploids. The results obtained do not support either the genome concept or the suggested mode of origin of *timopheevi*.

MATERIAL AND TECHNIQUES

The following parental species and varieties have been used in this investigation :—

$2^n = 14$ chromosomes
T. monococcum L. var. *vulgare* Körn.
$2^n = 28$ chromosomes
T. dicoccoides (a) Körn. var. *nudiglumis* Nabalek
T. dicoccoides (b) Körn. var. *kotschyanum* Perc.
T. dicoccum Schübl. var. *farrum* Körn.
T. polonicum L. var. *levissimum* Körn.
T. turgidum L. var. *iodurum* Körn.
T. turanicum Jacubz. (= *T. orientale* Perc.) var. *notabile* Perc.
T. carthlicum Nevski. (= *T. persicum* Vav.)
T. timopheevi Zhuk var. *typicum* Zhuk.

T. dicoccoides var. *nudiglumis* will be referred to as *dicoccoides* (a). Specimens of this variety were obtained from Mr J. B. Gillett (now at the Kew Herbarium, England) who had found the plants growing in Iraq, and following the botanical description of Nabalek (1929) they have been assigned to the variety *nudiglumis*. *T. dicoccoides* var. *kotschyanum* will be referred to as *dicoccoides* (b). Seeds of some of the F_1 hybrids and of the amphiploids were placed at my disposal by Dr G. D. H. Bell.

After a preliminary examination of meiosis on temporary aceto-carmine smears, all cytological observations were made on Feulgen squashes. Anthers were fixed in 1 : 3 acetic alcohol and stained according to the Feulgen technique. Permanent preparations mounted in " Euparal " were made after the schedule outlined in Darlington and La Cour (1947, p. 128). For a study of chromosome morphology in root tips, best results were obtained after pre-treatment for approximately three hours in a saturated solution of mono-bromo-naphthalene (O'Mara, 1948). This gave clearer chromosome figures than pre treatment with either low temperatures, paradichlorobenzene, chloral hydrate, or colchicine. Permanent preparations of root tips were also made by means of Feulgen squashes.

Unless otherwise stated, the figures on chromosome pairing are in each case based upon an analysis of 50 complete nuclei at the first metaphase of meiosis.

CHROMOSOME BEHAVIOUR IN F_1 SPECIES HYBRIDS

Chromosome pairing in six 28 chromosome F_1 hybrids between *timopheevi* and other 4*x* species of the genus *Triticum* is shown in table 1. The first five of these hybrids show a reduction from the possible 14 bivalents per cell and from the 29·94 chiasmata per nucleus found in the species *timopheevi*. In addition :—

carthlicum × *timopheevi* (4*x*) showed an average of 6·16 I, 9·44 II, 0·96 III and 0·02 IV.

timopheevi × *polonicum* (4*x*) showed an average of 7·76 I, 8·66 II, 0·92 III and 0·04 IV.

timopheevi × *monococcum* (3*x*) showed an average of 7·80 I, 6·09 II and 0·34 III.

The anthers did not dehisce in any of these F_1 hybrids and no seed was set. All these F_1 hybrids were therefore completely sterile.

Although previous workers have presented no adequate data for chiasma frequencies, these results broadly agree with those obtained by Lilienfeld and Kihara (1934) and Kostoff (1937). The 3*x* hybrid shows that the chromosome pairing in a hybrid between *timopheevi* and a diploid species of *Triticum* is not very different from some other 4*x* × 2*x* species hybrids in *Triticum*. The 4*x* hybrids show that there is a decreased chromosome pairing in hybrids between *timopheevi* and

other 4*x* species of *Triticum*, but there is no hybrid which even approaches an average of 14 univalents per cell. There is therefore always some chromosome pairing between the two chromosome sets of *timopheevi* and those of the other species of *Triticum*.

Chromosome pairing in the 4*x* F_1 hybrid *diococcoides* (a) × *timopheevi* (table 1) is, however, different from the chromosome pairing found in all the other 4*x* F_1 hybrids involving *timopheevi*. This hybrid shows 13·90 bivalents per cell and 28·54 chiasmata per nucleus. No chromosome bridges were found at anaphase and the tetrads appeared to be normal. Despite this apparently normal meiosis the anthers did not dehisce and under the glasshouse conditions of 1949 the hybrid plants were completely sterile.

TABLE 1

Chromosome pairing in F_1 hybrids of T. timopheevi *with other 4x species*

Hybrid	Mean chromosome pairing per cell					
	I	II	III	IV	Xta per nucleus	Term coeff.
timopheevi × *durum* *	3·90	10·55	1·00	0	**20·85**	*0·59*
dicoccum × *timopheevi*	4·98	10·30	0·78	0·02	**19·30**	*0·51*
timopheevi × *turanicum*	5·78	9·44	1·06	0·04	**17·88**	*0·57*
timopheevi × *turgidum*	6·32	9·04	1·12	0·06	**18·04**	*0·57*
dicoccoides (b) × *timopheevi*	5·62	10·00	0·74	0·04	**18·46**	*0·56*
dicoccoides (a) × *timopheevi*	0·20	13·90	0	0	**28·54**	*0·60*

* = 20 cells ; in all other hybrids 50 cells were analysed.
Xta = chiasmata. Term. coeff. = terminalisation coefficient.

In view of this result, hybrids were again made in 1949 using *dicoccoides* (a) on this occasion as both male and female parent. These hybrid plants were grown in two different lots in two open fields surrounded by many other fertile plants in order to ensure an ample opportunity for their pollination by foreign pollen.

Twenty-six F_1 plants were grown in 1950 and independently of whether *dicoccoides* (a) had been used as male or female parent the meiotic investigations confirmed the results which had been obtained in the previous year. Meiosis in the anthers was apparently normal in all cases, but none of the anthers dehisced. Degeneration of the gametes must therefore have occurred after the tetrad stage. From artificially opened mature anthers, a count of 500 pollen grains stained in aceto-carmine gave an estimate of 5 per cent. good pollen. Under the conditions of open pollination prevailing in the field in 1950 there was however some seed set. This was probably due to the greater viability of female gametes.

CHROMOSOME BEHAVIOUR IN AMPHIPLOIDS

Further evidence on the chromosome behaviour in hybrids of *timopheevi* can be obtained by a study of colchicine-derived amphiploids from the $4x$ F_1 hybrids. The chromosome pairing of six amphiploids (derived from the six F_1 hybrids described in table 1) is given in table 2.

Meiosis was studied in the first generation after colchicine treatment of the F_1 hybrid plants. Of particular interest is the 56 chromosome amphiploid *dicoccoides* (a) × *timopheevi* which had shown 13·90 bivalents in its 28 chromosome sterile F_1 hybrid. In contrast to its $4x$ F_1 hybrid,

TABLE 2

Chromosome pairing in 8x amphiploids of T. timopheevi

Amphiploid	Mean chromosome pairing per cell						
	I	II	III	IV	V/VI	Xta per nucleus	Term coeff.
timopheevi × *durum*	1·70	23·18	0·38	1·70	0	54·70	0·57
dicoccum × *timopheevi*	1·04	23·94	0·24	1·56	0·02	50·74	0·60
timopheevi × *turanicum*	0·86	23·50	0·26	1·84	0	54·22	0·56
timopheevi × *turgidum*	0·92	24·06	0·18	1·58	0·02	55·76	0·59
dicoccoides (b) × *timopheevi*	1·48	23·28	0·36	1·72	0	51·44	0·64
dicoccoides (a) × *timopheevi* *	1·47	21·10	0·47	2·73	0	51·44	0·64

* = 30 cells : in all other amphiploids 50 cells were analysed.

this $8x$ amphiploid *did* show dehiscence of the anthers. Two plants were examined for male and female fertility in 1950 :—

(i) A count of 1000 pollen grains stained in aceto-carmine gave an average of 75 per cent. good pollen.

(ii) Primary florets, open pollinated, of 125 spikelets showed a range of seed set per spike from 29 to 72 per cent. giving an average of 55 per cent. seed set.

The $8x$ amphiploid was therefore (like all the others) both male and female fertile.

The chiasma frequency per nucleus in the amphiploid *dicoccoides* (a) × *timopheevi* with 2·73 IV (54·8 per cent. of which formed rings) and 0·47 III, is the same as the chiasma frequency per nucleus in the amphiploid *dicoccoides* (b) × *timopheevi* with 1·72 IV (54·7 per cent. of which formed rings) and 0·36 III. Multivalent formation, therefore, did not influence the chiasma frequency per nucleus in these two amphiploids. In common with the other hybrids, multivalent formation in the amphiploid *dicoccoides* (a) × *timopheevi* is lower than bivalent formation in the F_1 hybrid. This is probably due to differential affinity (*cf.* Darlington, 1937).

CHROMOSOMAL STERILITY IN SPECIES HYBRIDS

Dobzhansky (1941) distinguishes between genic and chromosomal sterility in species hybrids. He points out that the principal source of evidence for the existence of chromosomal sterility in an F_1 hybrid is the behaviour of its allopolyploid. The production of a fertile amphiploid from the sterile F_1 *dicoccoides* (a) × *timopheevi* would thus indicate that the F_1 sterility is chromosomal, and the same applies to the other five amphiploids described in the previous section. The F_1 sterility of these other five amphiploids is, however, at least partly due to the formation of univalents and the subsequent abnormalities in meiosis, whereas the F_1 hybrid *dicoccoides* (a) × *timopheevi* was sterile despite an apparently normal meiosis.

TABLE 3

Chiasma frequency of parents, F_1 hybrid, and amphiploid
T. dicoccoides (*a*) × T. timopheevi

	Ploidy	Xta per nucleus
dicoccoides (a)	4*x*	29·06
timopheevi	,,	29·94
F_1 hybrid	,,	28·54
Theoretical amphiploid (sum of the parents)	8*x*	59·00
Experimentally produced amphiploid	,,	51·44

50 cells analysed in each species and hybrid.

Table 3 shows the chiasma frequency of the parent species, F_1 hybrid, and amphiploid *dicoccoides* (a) × *timopheevi*. This shows that the chiasma frequency of the F_1 hybrid was almost as high as that of the parent *dicoccoides* (a) and only slightly less than the chiasma frequency of the parent *timopheevi*. The observed amphiploid chiasma frequency was lower than the chiasma frequency derived from the sum of the two parent species. The ratio of observed to calculated chiasma frequency is 0·87 for chiasmata per nucleus. This ratio is comparable to that found in the other *Triticum* amphiploids, and in *Primula kewensis* (Upcott, 1939). The multivalent frequency in *Primula kewensis* is lower however than that found in the amphiploid *dicoccoides* (a) × *timopheevi*.

The behaviour of *Primula kewensis* has been explained by Darlington (1937) followed by Dobzhansky (1941) and Stebbbins (1950). It is assumed that the chromosomes of the two parent species are sufficiently alike to ensure chromosome pairing in the F_1 hybrid, but that non-homologous segments are involved in this apparently normal chromosome pairing. The gametes produced by the F_1 hybrid will then be inviable because recombination between the chromosomes of the two parent species has produced inviable combinations of genic

material. Pairing and segregation in the amphiploid produced by somatic doubling would, however, tend to produce gametes containing one complete set of chromosomes derived from one parent and one complete set of chromosomes derived from the other parent. These gametes would then be viable.

The type of chromosomal sterility in F_1 hybrids, which is brought about by chromosomal differences which do not materially affect metaphase chromosome pairing at meiosis, has been called cryptic structural hybridity by Stebbins (1945, 1950). The high degree of sterility in the F_1 hybrids, such as *timopheevi* × *durum* with a mean of 3·90 I per cell and in F_1 hybrids between *timopheevi* and hexaploid species of *Triticum*, may also be partly due to cryptic structural hybridity.

TABLE 4

Chromosome pairing in 4x F_1 hybrids of T. timopheevi, T. dicoccoides (*a*) *and* T. dicoccoides (*b*)

Hybrid	Mean chromosome pairing per cell					
	I	II	III	IV	Xta per nucleus	Term coeff.
dicoccoides (a) × *timopheevi* . .	0·20	13·90	0	0	**28·54**	*0·60*
dicoccoides (b) × *timopheevi* . .	5·62	10·00	0·74	0·04	**18·46**	*0·56*
dicoccoides (a) × *dicoccoides* (b) .	10·16	8·02	0·60	0	**13·36**	*0·52*

50 cells analysed in each hybrid.

Further evidence on these questions can be obtained indirectly. If chromosome pairing in the F_1 hybrid *dicoccoides* (a) × *timopheevi* involves non-homologous segments (as is indicated by the evidence presented above) these two parent forms may show a difference in chromosome pairing in other hybrid combinations. The amount of structural similarity sufficient to ensure good chromosome pairing between the two parent forms in the hybrid *dicoccoides* (a) × *timopheevi* may not be sufficient to ensure *equal* chromosome pairings when each of these parents is involved in other hybrid combinations. That this is actually the case is seen from the data in table 4.

With *dicoccoides* (b) as one of the parents, only 5·62 chromosomes remain unpaired in hybrids with *timopheevi* whereas 10·16 chromosomes remain unpaired in hybrids with *dicoccoides* (a). The possibility of genotypic (as opposed to structural) control of chromosome pairing producing the differences found in these two hybrids cannot be entirely ruled out. But these data on chromosome pairing can also be explained if some of the chromosomes of *dicoccoides* (a) and *timopheevi* are sufficiently unlike to give differences of pairing in their hybrids

with *dicoccoides* (b). These differences in pairing and the sterility of the F_1 hybrid *dicoccoides* (a) × *timopheevi* can thus both be explained by the existence of structural differences between the chromosomes of all three stocks.

THE GENOME CONCEPT AND THE ORIGIN OF TETRAPLOID *TRITICUM* SPECIES

Largely as a result of Kihara and his co-workers (Kihara, 1937, 1949) the concept of genome formulæ has become prominent within the sub-tribe *Triticinæ*. Metaphase chromosome pairing in hybrids is taken as an indication of chromosome homology and each chromosome set (called a genome) is given a specific formula. Some of the data from chromosome pairing can be used for the interpretation of phylogenetic relationships in conjunction with external plant morphology. Thus Kihara (1944) suggested that 14 chromosomes belonging to the chromosome sets of the 6*x* species of *Triticum* have been derived from the 14 chromosome species *Aegilops squarrosa*. This suggestion was experimentally confirmed by the actual synthesis of plants resembling 6*x* species of *Triticum* (MacFadden and Sears, 1946; Kihara and Lilienfeld, 1949).

Darlington (1937) has, however, stressed the undesirability of basing phylogenetic conclusions on chromosome pairing in hybrids. Dobzhansky (1941) has also pointed out that what is actually being studied is the chromosome pairing which is mainly determined by the gross structural arrangement of the chromosomes. The term genome implies that chromosome sets with the same genome formula contain the same gene complexes. There is, however, no evidence to suggest that the amount of genic differentiation is always proportional to the amount of structural differentiation which is able to influence chromosome pairing at the first metaphase of meiosis. Kihara (1937) has himself pointed out that there is no distinct dividing line between what is called a homologous and what is called a non-homologous genome, the one gradually merges into the other.

In most cases, metaphase chromosome pairing and chiasma formation in hybrids is assumed as being determined by the gross structural arrangements of the chromosomes. Phylogenetic speculations based only on the criterion of metaphase chromosome pairing can, however, lead to erroneous conclusions. The formulæ given to the chromosome sets of the 4*x* species of *Triticum* are a case in point.

The AG formula suggested by Lilienfeld and Kihara (1934) for *timopheevi* is also applied by Sears (1948) to the chromosome sets of *armeniacum*, and it is further suggested that the G chromosome set of both *armeniacum* and *timopheevi* is probably phylogenetically derived from a different species than the B chromosome set of the other tetraploids. The evidence for suggesting the formula G for one of the chromosome sets of *timopheevi* is based on the reduction of chromosome

pairing in 4*x* species hybrids involving *timopheevi*. The evidence for assigning the formula G to one of the chromosome sets of *armeniacum* is based on the data of Svetozarova (1939) that there is good chromosome pairing and apparently normal tetrads in the hybrid *timopheevi* × *armeniacum*. The data of Svetozarova (1939) however, also shows that despite an apparently almost normal meiosis the hybrid was sterile. The sterility in F_1 *timopheevi* × *armeniacum* may also be due to cryptic structural hybridity.

The chromosome behaviour of F_1 *timopheevi* × *armeniacum* is thus similar to that in F_1 *timopheevi* × *dicoccoides* (a) and in both cases meiosis would involve the pairing of chromosomes with non-homologous segments.

If one now follows the principles which are accepted in the giving of formulæ on the basis of metaphase chromosome pairing in hybrids, *dicoccoides* (a) would have to be given the formula AG in common with *timopheevi* and *armeniacum*. One would then be in a position either of having to elevate *dicoccoides* (a) into a new species (for which there is no justification) or of designating the variety *dicoccoides* (a) as AG and the variety *dicoccoides* (b) as AB. If the two varieties are designated as AB and AG one would then have to postulate that the tetraploid chromosome sets of these two varieties of *dicoccoides* are phylogenetically derived from two different species, which is highly improbable. This, therefore, shows the misleading conclusions that can be obtained when basing phylogenetic relationships only upon the amount of metaphase chromosome pairing at meiosis.

Considerable divergence in chromosome structure, as analysed by pairing at meiosis, has been found within the species *dicoccoides*. There is thus no reason to suppose that *timopheevi* and *armeniacum* may not also have diverged in the same way from an original 4*x* prototype. An examination of the chromosome morphology of *timopheevi* shows that, in common with the other 4*x* species of *Triticum*, it has at mitosis chromosomes with median or sub-median centromeres and four chromosomes with large satellites. It is not possible to identify with certainty all the individual chromosomes and chromosome measurements can differ appreciably in various varieties of the same species of *Triticum* (*cf.* Camara, 1947). The basic idiogram regarding the presence of median or submedian centromeres and the number of chromosomes with satellites is, however, the same in *timopheevi* as in the other 4*x* species. This evidence also conflicts with the suggestion that the tetraploid chromosome set of *timopheevi* has been phylogenetically derived from another species than the tetraploid chromosome set of e.g. *dicoccoides*.

The specimens designated as *dicoccoides* (a) are not morphologically identical with *armeniacum*. *Armeniacum*, among other characteristics, does not occur together with *Hordeum spontaneum*; it has no varieties with pubescent spikes; and it was found in Armenia and at Nakhichevan in Transcaucasia (Jukubziner, 1932; Tumanjan, 1934;

Makushina, 1938). Mr J. B. Gillett has informed me that there was considerable morphological variation in the specimens of *dicoccoides* which he found in Iraq. The plants were growing on the northern slopes of Handren Dagh above Jundiyan village a few miles east of Rowanduz. There were pubescent and glabrous forms of various colours and noticeable differences in the size of spike and general vigour. In contrast to *armeniacum* in Transcaucasia, the *dicoccoides* in Iraq was found growing together with *Hordeum spontaneum*. The considerable morphological range of *dicoccoides* in Iraq may on further cytological examination also show a range of chromosome differentiation from the *Syrio-palestinicum* types such as *dicoccoides* (b) to the cytologically differentiated types such as *dicoccoides* (a) and *timopheevi*. There is thus nothing improbable in the suggestion that all the 28 chromosome species of *Triticum* have originated from a common 28 chromosome prototype. The various stages of cytological differentiation may, in fact, still be in existence in Iraq.

SUMMARY

1. Two types of *T. dicoccoides* (a) and (b), have been found to differ in their chromsome structure. These types show that all the cytological differentiation among the 4*x* species of *Triticum* can be found within the species *dicoccoides*.

2. All the cytologically different 4*x* species of *Triticum* could thus have been derived from an original 28 chromosome prototype.

3. Tetraploid species hybrids with *T. timopheevi* show sterility presumably owing to recombination between chromosomes containing non-homologous segments.

4. Metaphase chromosome pairing in hybrids is not sufficient to assign distinct genome formulæ for the properties of different chromosome sets in various species.

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Plate

Microphotographs of polar motor cells at Metaphase I.
Feulgen staining. × 1800.

Plate

Microphotographs of pollen mother cells at Metaphase I.
Feulgen stained. ×1600.

FIG. 1.—4*x timopheevi* × *turgidum* 5 I, 10 II, 1 III.

FIG. 2.—4*x dicoccoides* (a) × *timopheevi* 14 II.

FIG. 3.—8*x dicoccum* × *timopheevi* 3 I, 19 II, 1 III, 3 IV.

THE CHROMOSOMES OF CHRYSANTHEMUM, II: GARDEN VARIETIES

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1. INTRODUCTION

New varieties of the garden chrysanthemum arise primarily from seed. They are propagated vegetatively and many give rise to bud sports in sequence and in parallel to give whole families of varieties. The original sports would naturally be chimæras and it is not surprising therefore that they often revert to the previous type. Whereas some varieties sport continually from the time of their origin, others remain stable for many years. Those considered in this account do, mostly, sport freely. Since varieties may remain stable for a considerable number of years and then suddenly sport it is probable that all varieties possess the ability to sport. The origin of bud sports is unpredictable.

Some confusion in naming has arisen as the same or similar sports have occurred and been propagated in different places under different names. Consequently there are, for example, several forms similar to, but not identical with, the original *Favourite Supreme* raised by Messrs A. G. Vinten. It might well be that each individual *variety* would be better termed a *sub-family* to include all its minor variants. The different *Chrysanthemum* sports are described in scattered numbers of the *R.H.S. Journal*—more particularly, for the *Favourite* family, in Vol. 63, 1938, pp. 139-141.

The object of this study is to discover the cause of sporting.

2. HISTORY

The first written reports of the cultivated *Chrysanthemum* date from about 500 B.C. but it had undoubtedly been grown for decoration previously. The original garden *Chrysanthemum* was probably a single, many-flowered variety similar to *C. indicum* which still occurs naturally in China and Japan. Cultivation has resulted in transformation of the corolla of individual florets in one of three directions. The small

five-toothed disc florets give rise either to broad flat ray florets or, alternatively, elongation without splitting results in quilled or tasselled forms. Increase in size of the disc florets produces anemone-centred types.

These changes have been accompanied by atrophy of the male sex organs. There is reduction in anther size and, in some cases, only the stalks remain, while in others all traces have disappeared. In A.D. 386 the *Chrysanthemum* reached Japan, via Korea, from China where it was first cultivated. Here it was selected and improved to give a great variation in form and colour. Most present-day forms of the flower were evolved in Japan over 1000 years ago.

In 1754 a small-flowered type was introduced into England from Holland where it had been cultivated as *Matricaria Japonica*. This plant was subsequently lost. In 1790 a large-flowered variety, " Old Purple ", was introduced (Curtis, 1796). Its inflorescence and general habit were similar to many present-day varieties and it was then considered a form of *C. indicum*. After 1820 more varieties were introduced from China and by 1826 forty-eight were known. In 1827 new forms were first produced by hybridisation and from these have arisen the incurved types of to-day. The first vegetative sport was noticed in 1832.

In 1843 Robert Fortune sent to England the first *Pompon*—the *Chusan Daisy*—from which numerous modern forms have been raised. He returned in 1861 with seven Japanese varieties, the forerunners of the so-called *Exhibition Japanese* types. The first early flowering varieties were selected from existing stocks in about 1850.

Since then there have been other introductions such as the *Korean* and *Midget* types. In 1930 McGregor sent from China a plant, similar to *C. indicum*, from the progeny of which were selected Sutton's *Charm* and *Cascade*.

The ancestry of many of these garden chrysanthemums is unknown. The similarity of chromosome size and form both between and within species removes one source of guidance. Cultivation and selection for so long may have resulted in plants bearing little resemblance to their ancestral species.

C. indicum, with its yellow flowers, is undoubtedly involved in the ancestry but whether it is the only species involved is uncertain. Hemsley (1889) considers *C. sinense* (*morifolium*) to be another likely parent. It is more robust than *C. indicum*, has tomentose leaves and ray florets differing in colour from the disc. Stapf (1933) considers the following species may also be involved : *C. erubescens*, a very distinct species with somewhat succulent like leaves and pink-rayed flower heads, together with *C. ornatum*, *C. japonense* and *C. makinoi*. He considers it improbable that oriental gardeners would ignore these naturally occurring species and concentrate on one only. He supposes that the garden *Chrysanthemum* has resulted from hybridisation and selection of them all.

All these species are hexaploid ($2n = 6x = 54$) excepting *C. makinoi* which is diploid ($2n = 18$). This latter can now be disregarded since the garden forms were, it seems, themselves originally hexaploid.

Other cultivated species of *Chrysanthemum* have been considered in the previous study.

3. CHROMOSOME NUMBERS OF VARIETIES

The somatic chromosome numbers of 65 varieties * vary between $2n = 47$-63, this including both $6x$ and $7x$ types ($x = 9$). Most

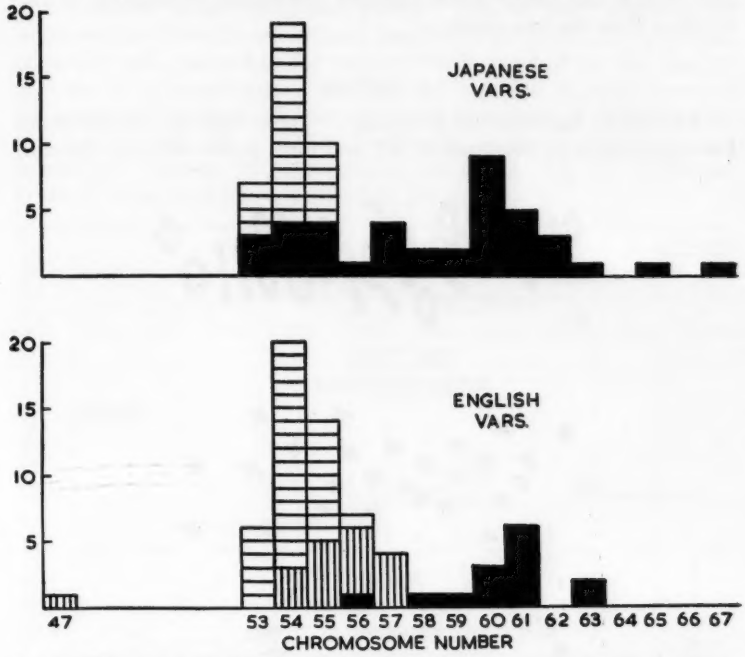

FIG. 1.—Chromosome numbers of varieties considered in the present account are shown in the lower graph. The upper graph is compiled from the results of Shimotomai (1933). Varieties are divided into three groups of increasing inflorescence size. Those shaded horizontally are less than 12 cm. in diameter, those vertically between 12 and 20 cm. and those in black over 20 cm. The large varieties of Shimotomai correspond to the medium and large English varieties.

varieties have between 54-56 chromosomes with the peak at $2n = 54$. Varieties have been separated into three groups of increasing inflorescence diameter. This increase in size is accompanied by increase in chromosome number (fig. 1).

* Root-tip squashes with the Feulgen technique were used, roots being pre-treated with mono-bromo-naphthalene for three hours (O'Mara, 1948). Acetic alcohol was the fixative and the hydrolysis time 15 mins. at 60° C. This method, though facilitating easy and rapid counting, has a disadvantage in that some cells become broken with inevitable loss of one or more chromosomes. Such cells are not considered.

Shimotomai (1933) carried out the only previous investigation of *Chrysanthemum* varieties. He divides them into two size groups only, one similar to the small English varieties, the other including those of medium and large size. In both English and Japanese varieties 54 is the most frequent number and in each the small-flowered forms have, mainly, between 53-55 chromosomes.

The range in chromosome number for medium and large varieties of the two areas together is 54-67. Medium-sized English varieties, with one exception, have 54 to 57. Large varieties have 56 to 63. Size groups and chromosome numbers correspond remarkably in the varieties from the two areas.

4. MEIOSIS

Meiosis in the varieties is regular. Those with 54 chromosomes invariably have 27 bivalents at MI and form pollen with 27 chromo-

FIG. 2.—(*a*) First metaphase and (*b*) First anaphase in *Market Gold* $2n = 55$. ×1800.

somes. Unbalanced forms usually have one or more univalent. Thus MI in varieties with 53 chromosomes have 26 pairs and one univalent, while forms with 55 have 27 pairs and one univalent (Fig. 2). The extra chromosome has not been seen to form a trivalent with a normal bivalent. Quadrivalents occurred in two cells; these may be due

either to associations of four homologous chromosomes or to interchanges.

Univalents, when present, normally divide at AI and may or may not be contained in the pollen. The pollen then has either 27 or 28 chromosomes. There is throughout a minimum of irregularity and the ripe pollen grains have uniform chromosome numbers.

5. THE ORIGIN OF NEW VARIETIES

Accompanying chromosome variation *between* varieties there is also variation *within* individual plants. Two or more chromosome numbers have been found within a single root (table 1). For example, of twelve cells counted in the variety *Wendy*, ten had 54, one had 53 and one 51 chromosomes. This type of variation is found in 20 of 65 varieties examined. While in its simplest form it involves only the gain or loss of a single chromosome, more complex changes involving a number of chromosomes are found (Fig 5). Different types of variation found are shown in fig. 3.

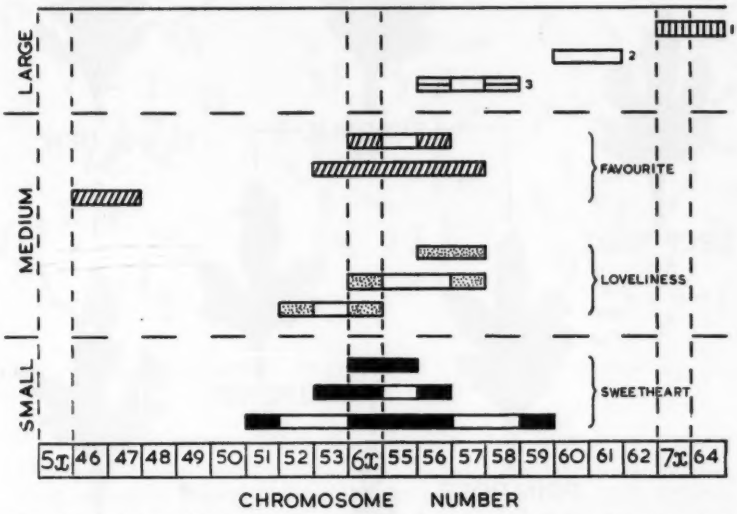

FIG. 3.—Variation within individuals of three families with small and medium-sized inflorescences is shown together with that in (1) *Birmingham*; (2) *Yellow Majestic*, and *Florence Reed* and (3) *Mrs R. C. Pulling*—these latter all being large varieties.

The questions then arise whether there is any connection between this type of variation and the origin of somatic sports, and whether there are differences between chromosome complements of the sports of a family that account for changes in flower colour. To settle these points, seven different sports from *The Favourite* were obtained. The vegetative ancestry of each was known. The original *Favourite*, a white-flowered plant, has given rise to three sports *Pink*, *Golden*, and

Favourite Supreme (the last pinkish bronze). Another five have arisen from these either directly or indirectly (fig. 4).

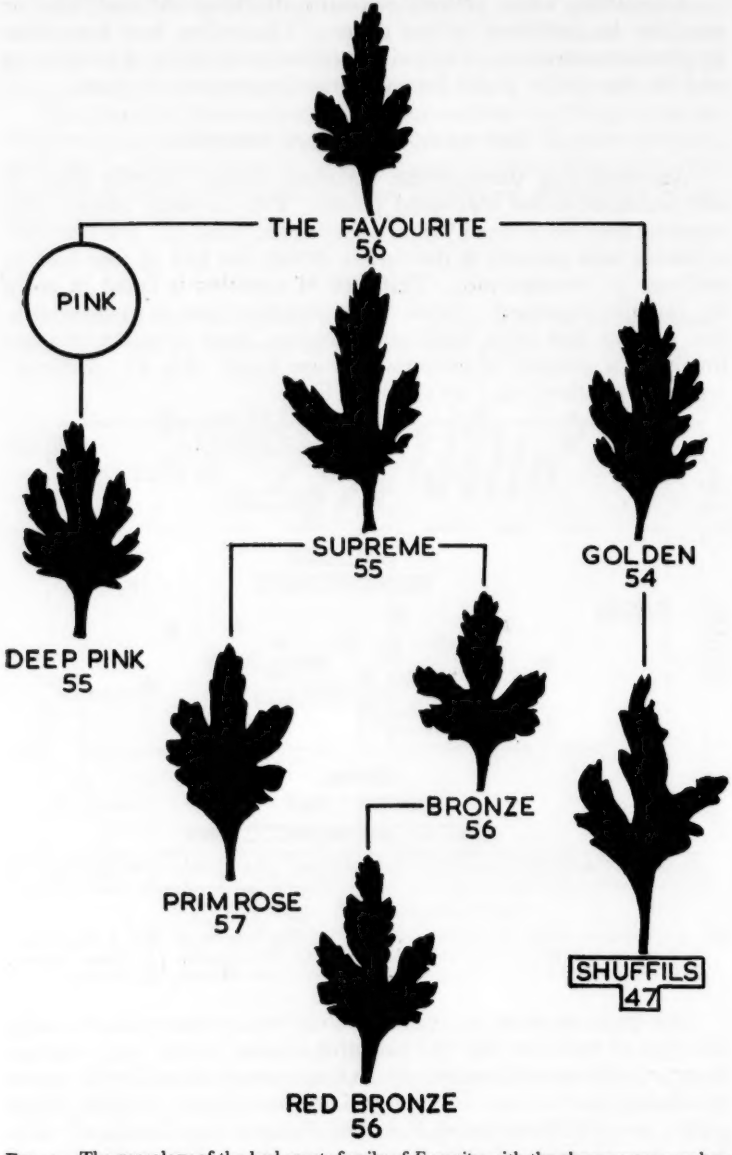

FIG. 4.—The genealogy of the bud sports family of *Favourites* with the chromosome number and leaf shape characteristic of each. Note *Shuffil's Favourite* with low chromosome number and aberrant leaf shape.

In *The Favourite* 20 cells had 56 and two had 54 chromosomes. Two of its three sports were examined and had 55 and 54 chromosomes. In one sport, *Golden Favourite* $2n = 54$, while cells with 53, 54, 55, 56 and 57 were found (table 1). From this plant arose *Shuffil's Favourite* ($2n = 47$) with reddish flowers. The loss of 7 chromosomes is accompanied by weakness and deformity. It also shows variation, having cells with 46 chromosomes.

A similar survey was carried out with two other families of sports from the *Sweetheart* and *Loveliness* parents (table 1). Results in these are similar to those in the *Favourites*, although in both the total range of chromosome numbers is smaller.

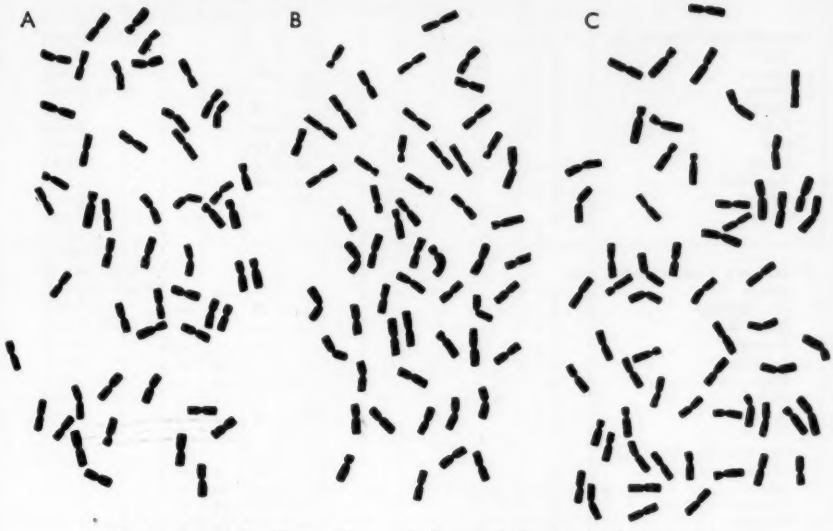

FIG. 5.—*Orange Sweetheart.* Three cells from a single root-tip (*a*) $2n = 51$; (*b*) $2n = 55$ and (*c*) $2n = 59$. ×1800.

Vegetative sports within these families thus arise from somatic variation in chromosome number. Sporting, together with chromosome variation brought about by sexual reproduction, will account for the range in chromosome number found throughout the varieties.

Although variation in chromosome number occurs from $6x$ to $7x$ there is no similar decrease towards $5x$. Chromosome loss would, normally, have a much greater effect than gain, and with it abnormalities would increase. Thus *Shuffil's Favourite* and similar plants would be less liable to survive. The absence of the $5x$ group is therefore to be expected.

There is throughout *Chrysanthemum* uniformity in form and size between the chromosomes of the basic complement (Dowrick, 1952). In hexaploid varieties it is impossible to say whether all nine chromo-

somes are present six times, or some seven times or more with others five or less. This is important when considering different colour sports of identical chromosome number. In, for example, both

TABLE 1

The frequency of different chromosome numbers within varieties of Chrysanthemum. L, *large* ; M, *medium* ; S, *small flowered*

Variety	Nos. of roots	Nos. of mitotic cells with different chromosome numbers												
		46	47	51	52	53	54	55	56	57	58	59	60	61
SWEETHEART FAMILY (S)														
Apricot	2					—	—	7	—					
Egerton	2					—	—	16	—					
Golden	2					—	—	—	10					
Peach	2					—	—	8	—					
Pearl	3					—	—	13	—					
Red	3					—	—	19	—					
Bronze	2					—	11	1	—					
Sweetheart	3					—	3	18	—					
Salmon	2					1	10	—	2					
Orange	2			1	—	—	1	18	6	—	—	1		
FAVOURITE FAMILY (M)														
Bronze	4						—	—	19	—				
Fav. Supreme	2						—	8	—	—				
Deep Pink	2						—	10	—	—				
Primrose	2						—	—	—	7				
Red Bronze	2						—	—	10	—				
White	4						2	—	20	—				
Shuffil's	4	2	10	—	—	—	—	—	—	—				
Golden	2					4	14	2	2	1				
LOVELINESS FAMILY (M)														
Amber	2						—	—	7	—				
Apricot	2						—	—	10	—				
Loveliness	2						—	—	11	—				
Primrose	2						—	—	11	—				
Purple	2						—	—	9	—				
Salmon	4						—	—	13	—				
Salmon Bronze	3						—	—	8	—				
White	2						—	—	10	2				
Bronze	3				3	—	11	—	—	—				
Lilac	3						5	—	—	13				
MAJESTIC FAMILY (L)														
Red Majestic	3							—	—	8	—	—	—	—
Yellow Majestic	3							—	—	—	—	—	1	10
Florence Reed	3							—	—	—	—	—	8	1

Egerton and *Red Sweetheart* the diploid number is 55 (fig. 6). But the flower colours are quite distinct. Presumably the same 55 chromosomes are not involved.

The present counts were made from roots. Young roots originate endogenously and arise from few cell layers. They do not necessarily give a picture of all the different numbers found in other parts of the

plant. The origin of new stems is more complex. Lateral branches are multicellular in origin, arising from many layers. Popham and Chan (1950) distinguish five zones in the shoot apex of the cultivated *Chrysanthemum*, differing both in the plane and frequency of their

TABLE 1 (*continued*)

Variety	Nos. of roots	Nos. of mitotic cells with different chromosome numbers										
				51	52	53	54	55				
INDIVIDUAL VARIETIES (S)												
Anastasia	4						10					
Apollo	2						8					
Autumn Gold	2						12					
Bronze Freda	2						11					
Cascade	2						15					
Charm	2						18					
Conqueror	2						7					
Finale	3						13					
Harvester	3						11					
Honeydew	2						12					
Imperial Yellow	2					8	—					
Ivory	2						8					
Jante Wells	3					10	—					
Market Gold	3						—	10				
Mayland Flame	3						9					
Red Planet	3					8	—					
Salmon Freda	4						11					
Snowfall	3						9					
Youth	2						8					
Mayford Red	3					8	1					
Irene Torrence	3					7	1					
Zenith	2					1	7					
Wendy	2			1	—	1	10					

Variety	Nos. of roots	55	56	57	58	59	60	61	62	63	64
INDIVIDUAL VARIETIES (L)											
Canada	4	—	—	—	—	—	—	11	—	—	—
Duchess of Kent	3	—	—	—	—	—	—	—	—	7	—
Golden Coralie	3	7	—	—	—	—	—	—	—	—	—
Goliath	3	—	—	—	—	—	—	9	—	—	—
James Bryant	3	—	—	—	—	—	—	9	—	—	—
Louis Barthou	3	—	—	—	8	—	—	—	—	—	—
Mrs H. Wells	3	—	—	—	—	9	—	—	—	—	—
Birmingham	2	—	—	—	—	—	—	—	—	9	1
Rise of Day	2	—	—	—	—	—	2	12	—	—	—
Mrs R. C. Pulling	3	—	11	—	1	—	—	—	—	—	—
Friendly Rival	3	10	—	1	—	—	—	—	—	—	—

divisions. The outer tunica of two to five cell layers mainly undergoes anticlinal divisions ; the outermost layer never divides periclinically, while the inner zones undergo divisions in all planes. The rate of division is, however, greater towards the centre of the shoot. The number of daughter cells perpetuating an error in division will, therefore, decrease the nearer the error is to the epidermis. But

wherever it occurs it results in a chimæra which at first is mericlinal and later periclinal, in its own lateral branches. The cell layers towards the centre of the stem are not contained in the petals, and changes in their chromosome numbers will probably not affect flower colour. Similarly anthocyanin is found only in the epidermis ; changes in that layer alone will affect the type or amount of anthocyanin produced.

Preliminary work on flower pigments of *Chrysanthemum* suggests that colour differences between different sports of a family are due

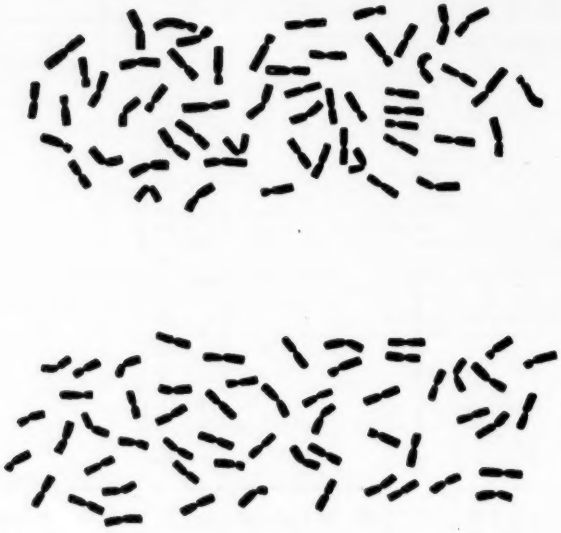

FIG. 6.—Cells of *Egerton* and *Red Sweetheart*. In both $2n = 55$. ×1800.

to quantitative differences between the pigments present (Dayton, unpub.). Qualitative differences could also occur without change in the type of genetic material present (Scott-Moncrieff, 1936).

It must be assumed that the different sports are, at first at least, chimæras. This characteristic will be retained by vegetative propagation. The continual throwing of some sports from particular varieties is thus to be expected, as for example, *Lizzie Adcock*, which continually arises from *Florrie Ford*.

Another case has been reported to me recently by Mr L. G. Atkins the Horticultural Advisory Officer of Lincolnshire. In a letter he says that a grower found that hot-water treatment at 40° C. for 20 mins. to protect the variety *Bronze Favourite* against eelworm resulted in the production of 20 per cent. of plants similar to, and which might be assigned to the same sub-family as, *Pink Favourite*.

It is probable that this treatment leads to the replacement of one layer by another at the growing tip. The original *Pink Favourite* arose directly from *White Favourite* and so here we have a method whereby the same, or similar, sports can arise in two quite distinct ways. Such parallel sports need not have the same chromosome number.

6. THE RATE AND METHOD OF ERRORS IN CHROMOSOME DIVISION

The question then arises how these variations come about. Observations have been made on mitotic anaphases and telophases in longitudinal sections of both root and stem tips. The rate and method of abnormality in stem tips only is considered here, as results are similar in both. Doubtful divisions were not scored.

TABLE 2

The rate of abnormal chromosome division found in different varieties of three families under constant temperature conditions (11·6° C.)

	Total no. of anaphases	No. of abnormalities
LOVELINESS FAMILY		
Amber	54	1
Apricot	135	2
Bronze	112	1
Lilac	88	1
Loveliness	274	3
Purple	20	0
Salmon Bronze	42	0
Salmon	59	0
White	53	1
SWEETHEART FAMILY		
Egerton	151	1
Golden	118	1
Pearl	192	3
Red	46	0
FAVOURITE FAMILY		
Red Bronze	217	4
White	53	0
Total	1614	18

Plants used in these tests were kept at a constant temperature of 11·6° C., both before and during the experiment. There were 18 abnormal divisions in 1614 analysed ; a frequency of 1·11 per cent.

It was then necessary to see whether environmental conditions influence the number of abnormal mitoses. Plants were placed in a constant temperature room at 23·5° C. for 3 days and then transferred to a refrigerator at 3·5° C. Root and stem tips were examined

24 and 48 hours after the temperature shock. A similar experiment with reciprocal temperature change was carried out simultaneously.

The first experiments had insufficient divisions for analysis. In the second there were 84 divisions after 24 hours, two of which showed errors. The results after 48 hours are summarised in table 3. Here

TABLE 3

The rate of chromosome abnormality at anaphase at a constant temperature of 11·6° C. and following a temperature shock intercalated between temperatures of 3·5° C. and 23·5° C.

Variety	Constant temperature 11·6° C.			Temperature shock		
	Total no. cells	No. of abnormal	Per cent. abnormal	Total no. cells	No. of abnormal	Per cent. abnormal
LOVELINESS FAMILY						
Amber	54	1	*1·85*	55	1	*1·82*
Bronze	112	1	*0·89*	121	2	*1·57*
Loveliness	274	3	*1·09*	71	1	*1·3*
Purple	20	...	...	86	2	*2·3*
Salmon Bronze	42	...	...	63	...	...
Total	502	5	*0·99*	396	6	*1·51*

the frequency of error is 1·5 per cent.; higher than under normal conditions.

It is to be expected, therefore, that chromosome variation in roots will depend partly on those external factors which influence the rate of abnormality. It must also be assumed that the variation within individuals, as shown in table 1, will not necessarily be complete.

TABLE 4

The frequency of different types of abnormal cell divisions in treated and untreated plants

	No. of cells		
	Non-disjunction	Laggard chromosomes	Sister reunion and fragments
Untreated	6	8	4
Treated	2	4	0

The types of anaphase abnormalities observed are shown in fig. 7 and plate 1. The most common result from non-disjunction of a single pair of chromosomes so that each daughter nucleus gains or loses one chromosome. Alternatively one or both of a pair of daughter chromosomes may lag in separation and are lost.

Plate

Chromosome numbers in root-tip cells

1. Orange Sweetheart 2n = 33. ×1400.

2. Orange Sweetheart 2n = 33. ×1400.

3. Orange Sweetheart 2n = 33. ×1400.

Plate

Chromosome numbers in root-tip cells

1. *Orange Sweetheart* $2n = 55$. ×1400.

3. *Orange Sweetheart* $2n = 51$. ×1400.

2. *Orange Sweetheart* $2n = 50$. ×1400.

Types of error in chromosome division in *Salmon Sweetheart*

4. Incomplete separation of daughter chromosomes at anaphase. ×1400.
5. Nondisjunction of a pair of chromosomes. ×1000.
6. Single laggard chromosome at telophase. ×1000.
7. Acentric fragment resulting from non-division of the end gene of the chromosome followed by breakage. ×650.

Anaphases and telophases can show incomplete separation of one or more pairs of chromosomes (fig. 7). The connection between two daughter chromosomes may continue after the new cell wall is laid down and may be present in the resting nucleus. Sometimes this is due to stickiness of the chromosome ends, which would eventually separate normally. Alternatively, however, these associations may be due to sister-reunion of the end gene to give a dicentric chromatid.

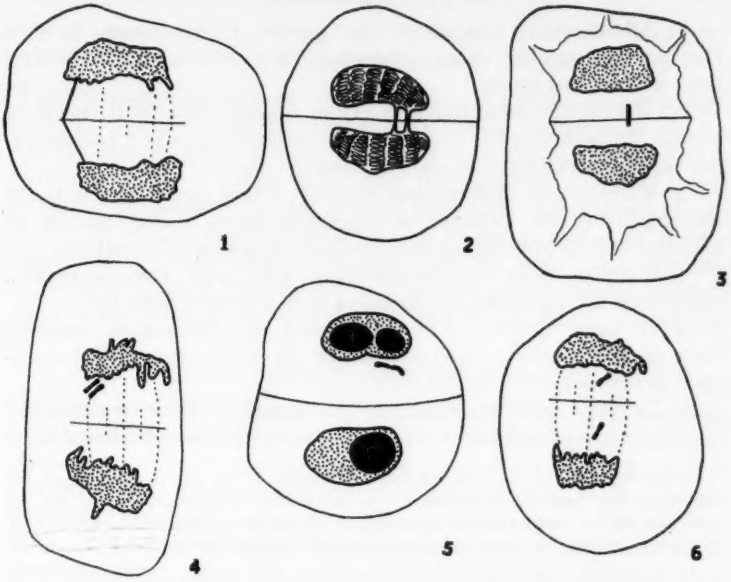

FIG. 7.—Errors of Division. Cells 1, 2 and 3 show stages of non-division of the end gene and stickiness. Cells 4, 5 and 6 show lagging chromosomes and non-disjunction. ×900.

Movement of the centromeres at anaphase followed by breakage would produce acentric fragments and short fragment chromosomes. Fragment chromosomes have not been found in English varieties, though two examples were reported by Shimotomai (1933) in plants where $2n = 54+$ f. and $2n = 59+$ f., and also in *C. lacustre* $2n = 196+2$ f. (Dowrick, 1952).*

7. OTHER VARIATION

Commercial growers are interested mainly in flower colour and shape, and they wish to change these characters only. Variation in chromosome number will not, however, be expected merely to change flower colour. Different sports of a family in fact proved to have characteristic leaf shapes (fig. 4) and also plant heights. Such changes and also chromosome variation can occur without affecting flower

* A small supernumerary euchromatic iso-chromosome has since been found in the large English variety *Turbulent* (2*n* 64+ f.) of unknown pedigree.

colour. The grower eliminates these to keep his stock constant in size and appearance.

Similarly it has been shown by Bailey (1951) that sports within a family differ in their susceptibility to disease. These differences may also be connected with variation in chromosome number.

8. SUMMARY

1. All ancestral species of the garden *Chrysanthemum* have a chromosome number of $2n = 6x = 54$. New varieties are produced from seed or bud sports.

2. The chromosome numbers of the English varieties lie between 47-63. In both English and Japanese varieties there is a correlation between inflorescence size and chromosome number.

3. Variation in chromosome number within plants accounts for the origin of new varieties as vegetative sports. The amount of variation differs in different varieties and according to conditions.

4. Various types of chromosome loss and non-disjunction, responsible for variation, are found in both root and stem tips.

5. In some families of sports varying in chromosome number, there are differences in (i) flower colour, (ii) leaf shape and (iii) resistance to disease.

6. In their meiotic behaviour the hexaploid varieties normally have 27 bivalents and the unbalanced forms a minimum of irregularity.

Acknowledgments.—I wish to express my thanks to Dr C. D. Darlington for suggesting this and other problems connected with *Chrysanthemum* and for his continual advice ; and also the Agricultural Research Council for the award of a scholarship during the tenure of which much of the work was undertaken.

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NATURAL HYBRIDS OF TWO SPECIES OF *ARCTOSTAPHYLOS* IN THE YOSEMITE REGION OF CALIFORNIA

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1. INTRODUCTION

THE purpose of the present note is to record a striking case of natural hybridisation of two species of manzanita bushes, *Arctostaphylos mariposa* Dudley and *A. patula* Greene, in and near Yosemite National Park, California. The weakness of this case, first reported by Epling (1947) is that the available data are derived from field observations in only a fraction of the total distribution area of the species, and are unsupported by experimental evidence. On the other hand, the case is remarkably clear and instructive since the environmental relationships of the parental species and of the hybrids are readily discernible.

2. THE PARENTS AND THE HYBRIDS

A. mariposa and *A. patula* are common and conspicuous members of the preclimax vegetation of the hillslopes in the Transition and in the lower portion of the Canadian life zones of the Sierra Nevada of California. In places they are abundant enough to form dense thickets of tall bushes or small trees on exposed slopes. They do not, however, grow on meadows and become depressed when forest shade develops above them. *A. mariposa* occurs at lower elevations than *A. patula*. According to Hall and Hall (1912) the former species occurs up to the elevation of 6000 feet, and the latter from 4500 to 9000 feet. In the region where the observations reported below have been made, *A. mariposa* extends from about 2500 to 6000 feet; and *A. patula* from approximately 4500 to 8000 feet above sea level. Taken at face value, these figures would indicate that the zone in which both species occur is about 1500 vertical feet. In reality it is usually narrower, because on slopes with southern exposure *A. mariposa* grows higher than on northern exposures. Conversely, the lower limit of *A. patula* extends lower on northern exposures than on southern. The soil drainage likewise influences the altitudinal limits of the species, rocky slopes being more accessible to *A. mariposa* than to *A. patula*. For these reasons, the altitudinal limits of the zone of overlap vary greatly from place to place. Occasionally the replacement of the species occurs without any overlap at all. This has been observed along a trail leading from the Rancheria Mountain to Hetch-Hetchy, in Yosemite Park. This trail first descends a mountainside with a north-eastern exposure, then emerges on a lower slope

with a southern exposure. Only *A. patula* has been seen on the north-east, only *A. mariposa* on the southern slope.

Morphologically the two species differ so clearly that they can be identified without hesitation even at a distance of one hundred feet or more (Jepson, 1923-25 ; Epling, 1947). *A. mariposa* has white-glaucous foliage which appears greenish-grey ; *A. patula*, bright green glabrous leaves. The former species is generally taller, more erect, and has the branchlets, the inflorescence, and the berries densely covered with glandular pubescence which makes them very sticky to touch. *A. patula* is usually lower, frequently semi-prostrate, and its inflorescent is only minutely pubescent, the berries large, glabrous or nearly so, never sticky. The leaves of *A. mariposa* are on the average smaller (mostly 2 to 4 cm. long) than the *A. patula* (3 to 5 cm. and even more). The stems of *A. patula* form a " burl ", *i.e.* an irregularly globose body, under the soil surface, which crown-sprouts after fire. *A. mariposa* does not have this property.

The hybrid bushes are on the whole intermediate between the parents, but somewhat closer to *A. patula* in the conspicuous traits. Their leaves are bright green, slightly glaucous and therefore not glossy. The leaf size is only slightly smaller than in *A. patula*. The manner of growth approaches that in *A. mariposa* rather than that in *A. patula*. The inflorescence is moderately pubescent but not glandular and not sticky. The berries are almost glabrous, like in *A. patula*. The variation in the hybrids is not any greater than it is in the parental species, and there is no overlapping at all, making the hybrids a morphological array which can be separated without hesitation from those of the parents (Epling, 1947).

3. A SAMPLE TRANSECT

Observations were made on the relative frequencies of the individuals of the two species and of the hybrids in several localities in the Yosemite region. Usually a trail or a road was selected leading from the lower elevations where only *A. mariposa* is found to the higher areas where only *A. patula* is encountered. The bushes on either side of the trail were classified as to species. On two such transects counts were made of the numbers of bushes of the three kinds growing within five metres on either side of the trail. The trail was subdivided into sections 100 paces long, the section boundaries marked, and the bushes counted and recorded. The direction of each section of the trail was determined with the aid of a compass, and a rough map was prepared. The elevation above the sea level of the different parts of the trail was determined with the aid of an aircraft altimeter. Notes were made on the vegetation in each section, as well as on the characteristics of the soil, slope, etc.

One of the transects is reproduced in fig. 1. The individuals of *A. patula* are marked by black circles, *A. mariposa* with white ones,

and hybrids with half black and half white. The trail leads from Mather to the Cottonwood Meadow in the Yosemite Park. The counts were started at the elevation of 4800 feet and finished at 5500 feet. In all, 745 *A. mariposa*, 166 *A. patula*, and 37 hybrids were counted. On this particular transect very few young bushes were found, a majority being mature fruiting individuals. Below 4800 feet many *A. mariposa* and a single hybrid bush were noted, and above 5500 feet numerous *A. patula* and also a single hybrid bush occur along the trail. The part of the trail along which counts were made thus covers the transition between the distribution areas of the two species.

Section 1 of the transect (fig. 1) abuts a flat densely overgrown with young yellow pines (*Pinus ponderosa* Dougl.) and incense cedars (*Libocedrus decurrens* Ferr.). Sections 1-4 climb up a slope of a hill, mostly exposed to the sun, but with few scattered yellow pines. Here are found 192 bushes of *A. mariposa*, no *A. patula*, and 4 hybrids. Sections 5-7 cover fairly flat ground with deeper soil and scattered oaks (*Quercus Kellogii* Newb.), cedars and pines. There 6 hybrids and 109 *A. mariposa* are found. Sections 8 and 9, elevation 4900 feet, begin to climb up a fairly gentle slope with scattered oaks, pines and cedars. There another eight hybrids are recorded. Sections 10

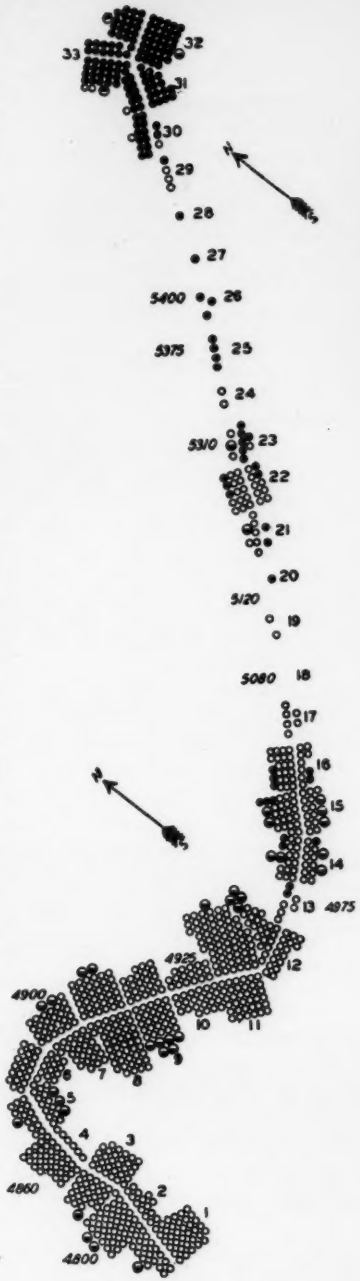

FIG. 1.—A sample transect of the altitudinal zone in which *Arctostaphylos mariposa* (open circles), *A. patula* (solid black circles), and their hybrids (black-and-white circles) occur. The numerals indicate the numbered sections of the transects and the elevations, in feet above the sea level.

and 11 are on a much steeper and rocky slope exposed to the south and devoid of shade. Numerous *A. mariposa* grow on this slope, but the single hybrid is found close to the boundary of Section 12, where the conditions change. The absence of hybrids in Sections 10 and 11 is probably significant—they are less well adapted than *A. mariposa* to grow on hot and exposed slopes at this elevation.

Sections 12 to 16 enter the mouth of a canyon, with some large pines, cedars and oaks, particularly to the right of the trail, and with less rocky soil. There 129 *A. mariposa*, 13 hybrids, and the first 13 bushes of *A. patula* have been counted. Both the hybrids and *A. patula* grow in relatively flat, more protected locations with some shade from the larger trees. Sections 17 to 20 are unfavourable for *Arctostaphylos*, being shaded by a dense growth of yellow and sugar pines (*Pinus Lambertiana* Dougl.), cedar, white fir (*Abies concolor* Linde), oak and Douglas fir (*Pseudotsuga taxifolia* Lamb.). The few *A. mariposa* and the single *A. patula* are depressed individuals. Sections 21 to 24 are climbing up along the bottom of a fairly steep-walled canyon with a small impermanent stream at the bottom. The slope to the right (south-east) of the trail is much more densely wooded than that on the left. Almost all *Arctostaphylos* bushes are growing on the left slope of the canyon (although not necessarily to the left of the trail). Both species and hybrids are found, with *A. patula* and the hybrids clearly selecting the less dry and more protected situations.

Sections 25-29 are in the head of the canyon, where the sides are less high and less steep. There is much forest shade, the *Arctostaphylos* bushes being not numerous near the trail but more abundant higher up on the left slope. Examination of these bushes (not entered in fig. 1) discloses that the upper and exposed parts of the slope have chiefly *A. mariposa* and a few hybrids, while along the trail *A. patula* predominates. Finally, Sections 30-33 are on a small plateau at the elevation of approximately 5500 feet. On this plateau, and higher up on the Sierra slope, *A. patula* is clearly the predominant species. Some hybrids, and the last *A. mariposa*, occur, however, on this plateau.

4. OTHER TRANSECTS

Conditions similar to the ones described above have been observed on other transects as well. Within the zone of the overlap, *A. mariposa* grows relatively more frequently in hot, exposed, or rocky situations, while *A. patula* and the hybrids occur in more protected, less arid places, frequently with some shade. And no matter how wide or narrow is the zone of the overlap, always a decided majority of the bushes belong to the two parental species, with hybrids in a minority. Along the road from Mather to Aspen Valley the zone of the overlap extends from the elevation of about 4900 to 6000 feet and for about three miles horizontally. Counts were made of bushes within five metres on either side of the road. *A. patula* was represented by 1051

individuals, *A. mariposa* by 110, and only 27 hybrids were found. The predominance of *A. patula* on this transect is due to the fact that its lower part has too much shade to support numerous *Arctostaphylos*. A few miles away from there, on a margin of Ackerson Meadow which was logged and partly burned in 1946, numerous young bushes are found. Our counts showed that less than 1 per cent. among them are hybrids, and about 80 per cent. are *A. mariposa*. It would be interesting to compare the relative frequencies of the pure species and the hybrids in a decade or a larger time interval, since it is possible that the hybrids may be eliminated at rates greater than the pure species.

5. CONCLUSIONS

A. mariposa and *A. patula* are two Mendelian populations which are adapted to occupy related but distinctly different adaptive niches. The former is superior under the more arid conditions of the lower, and the latter under the less arid ones of the intermediate elevations, in the Sierra Nevada of California. The two populations must clearly be regarded as specifically rather than only racially distinct. This is because the gene exchange between them is clearly not effective enough to erase the barriers to further gene flow. Their genetic systems are almost completely closed. This fact is reflected on the morphological surface to permit classifying the individuals observed in three discrete arrays—that of *A. mariposa*, of *A. patula*, and that of the hybrids. The first two arrays are much larger than the third one, even in the zone of the geographic and environmental overlap where the hybrids occur.

It should be stressed that the hybrids do not seem to be sterile. At any rate, the hybrid bushes produce crops of berries just as abundantly as do the parental species. The seeds are visibly normal, but no germination experiments have been made. This raises the question of what prevents the spread of the hybrids and the swamping of the species boundary, at least in the zone of the distributional overlap, which would degrade the species to races. A great majority of the hybrids are, as stated above, a discrete array which is not noticeably more variable than the parental species. This suggests that they are the F_1 hybrid generation, although one cannot exclude the possibility that a small minority of them may be F_2 or backcross products. Bushes which, on morphological grounds, appear to be backcross individuals are rare, although they are found. In the part of the Yosemite region in which the observations were made, eight bushes have been noted which, with varying degrees of assurance, can be described as intermediates between the F_1 hybrids and the parents. Of these, six suggest backcrosses to *A. mariposa* and two to *A. patula*. Four are fairly large, and they have been observed to produce berries in several successive seasons.

Efforts have been made to detect the possible introgression of

the genes of *A. mariposa* into *A. patula*, and vice versa, particularly in the zone of the overlap. Although the writer does not claim an "ability to spot introgression in the field, sometimes almost instantly and frequently in organisms with which one was unfamiliar" (Anderson, 1951), the populations of both species were inspected within and outside the zone of the overlap. Such inspection shows, to an increasing degree as one becomes more familiar with the plants, the existence of local, intercolonial variations in all sorts of traits. How much of this variation, is genotypic and how much purely environmental is, of course, impossible to tell. What is important for our purpose is that no indication was observed of mutual approximation of the species in the zone of the overlap, except, possibly, that *A. patula* tends to be more erect than it is further up the Sierran slope. The erectness is a trait characteristic of *A. mariposa*.

It is quite possible that a narrow channel for gene exchange between the species is preserved. Morphological observation could not exclude this possibility entirely, especially since backcrosses of the hybrids to *A. patula* might produce progenies that would be difficult to recognise. The important fact is that the gene exchange, if it occurs, does not furnish in the *Arctostaphylos* case genetic building blocks for adaptive modification of local populations. Since both *A. mariposa* and *A. patula* come up most abundantly on disturbed soils after burning or logging the forest, human activities have doubtless increased the sizes of the populations of both species as well as opportunities for species crosses. It is, however, unlikely that no hybrids at all were found until men came. If so, the absence of clear introgression effects suggests that the two species are coherent genetic systems which form a reasonably fit F_1 hybrid, but which suffer a breakdown in F_2 and in backcrosses, with natural selection eliminating most or all recombination products. Formation of some viable and fertile hybrids between species in nature does not necessarily erase the reproductive isolation which keeps their genetic systems separate.

6. SUMMARY

Two species of manzanita bushes, *Arctostaphylos mariposa* and *A. patula*, form some natural hybrids. The former species occurs at lower elevations and in drier and more exposed sites than the latter, but in a fairly narrow altitudinal belt the two occur together. The hybrids, which are mostly F_1 and much less often F_2 or backcross products, never form more than 10 per cent. of the population of the region in or near which both parental species also occur (*cf.* fig. 1). In that region, the parental species and the hybrids tend to occupy somewhat different habitats. There are no indications of extensive introgression of genes of *A. mariposa* into *A. patula* or vice versa. It is suggested that an important isolating mechanism which keeps the

gene pools of these species closed systems is adaptive inferiority of most products of gene recombination.

Acknowledgments.—Thanks are due to Professor G. L. Stebbins, who first called the attention of the writer to the *Arctostaphylos* situation in 1945 ; to Professor C. Epling in co-operation with whom the first observations were made in 1945 ; to Miss Sophie Dobzhansky, who, in 1951, shared the work of making the counts of the plants and preparing the maps of the transects ; and to Dr Jens Clausen and his colleagues of the Division of Plant Biology of the Carnegie Institution of Washington, whose hospitality at Mather furnished the opportunity to carry out the observations here reported.

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THE VARIATION IN STRENGTH OF THE HUMAN BLOOD GROUP *P*

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1. INTRODUCTION

Soon after their discovery (1) of the blood group known by the genetical symbols *P*, *p*, Landsteiner and Levine called attention to the great variability of the *P* reaction with anti-*P* sera. This variability has proved very troublesome, and for some years the validity of estimates of gene frequencies was in some doubt, owing to the possibility that an unknown proportion of weak positive reactions were passing as negative. Moreover, there is still no anti-*p* reagent to supplement the typing antibody first discovered.

Owing to the improved technique developed by Jonsson and Henningsen (2), and the use of potent testing fluids, the difficulty of distinguishing weakly reacting blood containing *P* from the recessive form *pp* is now believed to be overcome. The causes of variation in strength are, however, still obscure. Henningsen has indeed suggested (3) that his data may be interpreted as showing a series of four alleles :—

p	47 per cent.
P weak	10 ,,
P medium	40 ,,
P strong	3 ,,
	100 ,,

After examining the data on which this suggestion was based, I suggested in correspondence that a more detailed examination of this fine body of material might be profitable. Dr Henningsen, therefore, very cordially sent me further details, and some additional observations, together with information as to factors such as age of the donor, freshness of the sample, etc., which have guided me in the choice of the further calculations I have made. Especially because my conclusions diverge somewhat from those to which Henningsen was first led, I should like to make it clear that my enquiry rests exclusively on his work, and has been made possible only by his courtesy.

2. THE FAMILY DATA

In the case of 221 families both parents were classified in four phenotypic classes as Strong, Medium, Weak and Negative. As the frequency distribution for children differed considerably from that

for the parents, I have felt on safe ground in recognising for these only the distinction of Positive and Negative. This distinction is sufficient to allow of an estimation of limited but useful precision of the proportion of each phenotypic class of parent who are heterozygous, meaning by this that they contain the negative gene *p*, whatever allelomorph it may be combined with.

For this purpose we need to know for each of the nine phenotypic classes of mating, which might show segregation among the children : (i) How many matings have yielded at least one negative child, (ii) in the case of matings with no negative child, how many children have been tested. The number of children in families of the first class is a matter of indifference, since any one negative child proves both parents to be heterozygous, if not known to be themselves negative, and further information can tell us no more than this. In the cases of families with no negative children on the contrary, the larger the family the higher is the probability that at least one parent is homozygous.

With these considerations in view, the whole of the data may be summarised compactly as in table 1.

TABLE 1

Type of mating	Numbers of matings with negative children	Numbers of tested children in matings with no negative children	Numbers of matings with no negative children	Total numbers of matings
Strong—Strong . .	3	$1^2\,2^5\,3\,4^2\,6$	11	14
Strong—Medium .	2	$1^3\,2^{10}\,3^3\,4^3\,5\,6^2\,13$	35	37
Strong—Weak . .	0	$1^2\,2^3\,3^2$	7	7
Strong—Negative .	5	$1^5\,2^3\,3^3\,4^2\,5^3$	16	21
Medium—Medium .	16	$1^9\,2^9\,3^{10}\,4^4\,5^3\,6\,7$	37	53
Medium—Weak .	6	$1^2\,2^6\,3^3\,4^3\,6^2$	16	22
Medium—Negative .	23	$1^8\,2^8\,3\,4\,8,\,10$	20	43
Weak—Weak . .	1	2	1	2
Weak—Negative .	8	1	1	9
Negative—Negative .	13	...	0	13
Total . .	77	...	144	221

Of the total 442 parents tested 99 were negative. The proportion of recessive genes is estimated to be

$$\sqrt{99/442} = 47{\cdot}3267 \text{ per cent.}$$

Consequently, the frequency of positive genes of all possible sorts is 52·6733 per cent., and the proportion of persons with two such genes, who may be called homozygous positives, is

$$(52{\cdot}6733 \text{ per cent.})^2 = 27{\cdot}745 \text{ per cent.}$$

We may, therefore, using the proportion of negative parents only, estimate the number of homozygous positives to be

$$442 \times 27{\cdot}745 \text{ per cent.} = 122{\cdot}6.$$

These must be distributed in some way among the 93 strong, 208 medium and 42 weak recorded. If estimates of the numbers of homozygotes in each of these classes give a concordant estimated total, without using the number of parents negative, this will be a genuine confirmation of the consistency of the data, and of the appropriateness of the method of interpretation.

3. THEORY OF THE CALCULATIONS

If the probability of each child being positive is 3/4, the probability that none will be negative out of s is $(3/4)^s$, and the probability of one at least being negative is

$$u_s = 1-(3/4)^s.$$

Similarly, if, as in a backcross, the probability for each child is 1/2, the probability of at least one negative child is

$$v_s = 1-(1/2)^s.$$

These auxiliary quantities, so far as they are needed for the actual family sizes recorded are shown in table 2.

TABLE 2

Values of u_s *and* v_s *for various sizes of family*

Size of family	u_s $1-(3/4)^s$	Size of family	v_s $1-(1/2)^s$
1	0·25	1	0·5
2	0·4375	2	0·75
3	0·578125	3	0·875
4	0·683594	4	0·9375
5	0·762695	5	0·96875
6	0·822021	8	0·996094
7	0·869680	10	0·999024
13	0·976243		

If p_1 is the proportion of heterozygotes among individuals classified as Strong, p_2 the proportion among the Medium, and p_3 among the Weak, the proportion of the various mating types capable of giving Negative children can be easily calculated. *E.g.* in the mating type Strong mated to Strong, the proportion of matings in which both parents are heterozygous will be

$$p_1^2,$$

and the probability of a family of s having at least one Negative child will be

$$p_1^2 u_s,$$

while the probability of such a family having no Negative child will be

$$1-p_1^2 u_s.$$

Efficient scores for families of s children of these two kinds are found by taking the logarithms, and differentiating with respect to the unknown parameter p_1. Thus we have

Score for family with at least one Negative child $2/p_1$

Score for family with no Negative child $\dfrac{-2p_1u_s}{(1-p_1^2u_s)}$

In connection with these scores we shall also be concerned to evaluate the amount of information concerning p_1 supplied by the family in question, and this may be evaluated from the differential coefficient of the score with respect to p_1, taken with reversed sign.

So, for a family of s children from a mating with both parents Strong, we have

From a family with at least one Negative child, information

$$2/p_1^2 = S/p_1$$

From a family with no Negative child $-S/p_1+S^2$.

For a mating of Strong and Medium parents, we have correspondingly the probability

$$p_1p_2u_s$$

of at least one Negative child, and

$$1-p_1p_2u_s$$

of no Negative child. Such families are to be scored both for p_1 and for p_2, the scores being

	For p_1	For p_2
Negative child	$1/p_1$	$1/p_2$
No Negative child	$-p_2u_s/(1-p_1p_2u_s)$	$-p_1u_s/(1-p_1p_2u_s)$

From these again the amounts of information are S_1/p_1 and S_2/p_2 for families with a Negative child, while in the alternative case they are

$$S_1^2, \quad S_1S_2, \quad S_2^2$$

the middle term being the cross information for the simultaneous estimation of p_1 and p_2.

A third case is offered by the mating Strong with Negative. Here the probabilities are

	p_1v_s	and	$1-p_1v_s$
with scores	$1/p_1$	and	$v_s/(1-p_1v_s)$

and amounts of information

S/p_1	and	S^2

respectively.

Since, on the whole, parents classified as Weak produce Negative children more rather than less frequently than would be expected if

all were heterozygous, we shall simplify the calculations by taking $p_3 = 1$. In this case the matings Strong by Weak and Medium by Weak will be scored just as are Strong by Negative and Medium by Negative, save that u_s will now be used in place of v_s.

4. THE ESTIMATION OF THE PROPORTIONS HOMOZYGOUS

Table 3 gives in detail the scores and amounts of information credited to each class of family according to the type of mating involved. The trial values employed, 1/3 for p_1, and 0·7 for p_2, were known to be very near the values of maximum likelihood. The total scores for p_1 and p_2 are found to be

$$0{\cdot}4383 \quad \text{and} \quad 0{\cdot}5286.$$

The totals for all families also gives the information matrix

$$\begin{Bmatrix} 158{\cdot}4093 & 11{\cdot}9189 \\ 11{\cdot}9189 & 306{\cdot}3893 \end{Bmatrix},$$

so that adjustments δp_1 and δp_2 to the trial value may be calculated from the equations,

$$\begin{aligned} 158{\cdot}4093\,\delta p_1 + 11{\cdot}9189\,\delta p_2 &= 0{\cdot}4383 \\ 11{\cdot}9189\,\delta p_1 + 306{\cdot}3893\,\delta p_2 &= 0{\cdot}5286. \end{aligned}$$

The covariance matrix is found by inverting the information matrix, and multiplied by 10,000 this is

$$\begin{Bmatrix} 63{\cdot}3129 & -2{\cdot}4629 \\ -2{\cdot}4629 & 32{\cdot}7340 \end{Bmatrix},$$

giving the adjustments

δp_1 0·264 per cent., δp_2 0·162 per cent.,

and the corrected estimates

p_1 33·597 per cent., p_2 70·162 per cent.,

with standard errors

$$\pm 7{\cdot}957 \quad \text{and} \quad \pm 5{\cdot}721.$$

We may now partition the 442 parents observed, both phenotypically and genotypically as follows :—

	Homozygous	Heterozygous	Total
Strong	61·8	31·2	93
Medium	62·1	145·9	208
Weak	0	42·0	42
Total . . .	123·9	219·1	343

The agreement between the number of homozygotes estimated from the families without reference to negative parents, namely

123·9, with 122·6 the number estimated from the number of negative parents without reference to the families, is quite striking.

TABLE 3

Scores for each class of family, $p_1 = 0{\cdot}3$, $p_2 = 0{\cdot}7$

(*a*) Scoring for p_1

	Families	Score p_1	$i_{p_1 p_1}$
Strong mated to Strong			
With Negative children	3	+18·0000	65·6313
Without Negative children: 1 child	2	−0·3429	0·0588
2 children	5	−1·5328	0·4699
3 ,,	1	−0·4119	0·1697
4 ,,	2	−0·9864	0·4865
6 ,,	1	−0·6031	0·3637
		+14·1229	67·1799
Strong mated to Negative			
With Negative children	5	+15·0000	45·0000
Without Negative children: 1 child	5	−3·0000	1·8000
2 children	3	−3·0000	3·0000
3 ,,	3	−3·7059	4·5779
4 ,,	2	−2·7273	3·7191
5 ,,	3	−4·2923	6·1413
		−1·7255	64·2383
Strong mated to Weak			
With Negative children	0	...	...
Without Negative children: 1 child	2	−0·5455	0·1488
2 children	3	−1·5366	0·7870
3 ,,	2	−1·4323	1·0257
		−3·5144	1·9615
Strong mated to Medium			
With Negative children	2	+6·0000	18·0000
Without Negative children: 1 child	8	−1·4867	0·2763
2 children	10	−3·4107	1·1633
3 ,,	8	−3·7423	1·7506
4 ,,	5	−2·8466	1·6206
5 ,,	1	−0·6495	0·4219
6 ,,	2	−1·4239	1·0137
13 ,,	1	−0·8850	0·7832
		−8·444	25·0296
		$i_{p_1 p_2}$	11·9189
		$i_{p_2 p_2}$	5·6756
		Score p_2	−4·0213

5. DISCUSSION

It is clearly demonstrated in the foregoing sections that one important cause of variation in the strength of the *P* reaction lies simply in the difference between persons with two and persons with only one positive gene. Other genetical causes are possible, but it is not easy, without family studies freed from the quantitative effects of age, even to prove their existence, still less to exhibit their nature.

Strength of reaction is generally observed to be associated in parents and offspring. Nevertheless, the view that all causes other than homozygosity were exogenic could not be disproved without a quantitative study showing that the degree of association observed is really greater than that to be expected merely from the association of homozygosity in parents and children.

TABLE 3 (*continued*)

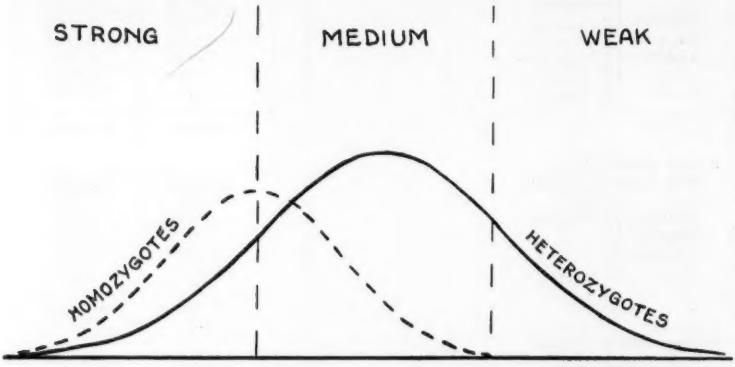
(*b*) Scoring for p_2

	Families	Score p_2	$i_{p_2p_1}$
Strong mated to Medium	...	−4·0213	5·6756
Medium mated to Medium			
With Negative children	16	+45·7143	117·9046
Without Negative children: 1 child	9	−3·5897	1·4318
Without Negative children: 2 children	9	−7·0169	5·4705
Without Negative children: 3 ,, ...	10	−11·2928	12·7527
Without Negative children: 4 ,, ...	4	−5·7562	8·2835
Without Negative children: 5 ,, ...	3	−5·1148	8·7204
Without Negative children: 6 ,, ...	1	−1·9270	3·7133
Without Negative children: 7 ,, ...	1	−2·1217	4·5016
		+8·8954	162·7784
Medium mated to Weak			
With Negative children	6	+8·5714	12·2449
Without Negative children: 1 child	2	−0·6061	0·1837
Without Negative children: 2 children	6	−3·7838	2·3862
Without Negative children: 3 ,, ...	3	−2·9134	2·8293
Without Negative children: 4 ,, ...	3	−3·9326	5·1551
Without Negative children: 6 ,, ...	2	−3·8721	7·4966
		−6·5366	30·2958
Medium mated to Negative			
With Negative children	23	+32·8571	46·9387
Without Negative children: 1 child	8	−6·1538	4·7337
Without Negative children: 2 children	8	−12·6316	19·9447
Without Negative children: 3 ,, ...	1	−2·2581	5·0990
Without Negative children: 5 ,, ...	1	−3·0097	9·0583
Without Negative children: 8 ,, ...	1	−3·2903	10·8261
Without Negative children: 10 ,, ...	1	−3·3225	11·0390
		+2·1911	107·6395

Without being wholly exogenic the remaining variation in strength of reaction might be due partly to genes of small effect acting as cumulative factors, or to multiple alleles at the *P* locus. In the latter case there might be, for example, only two such positive alleles, or equally there might be very many with various grades of strength. Whichever of these views may be favoured, the existence of considerable non-genetic influence must be admitted, and this consideration should prevent any tendency to identify arbitrary, though striking, phenotypic grades with genetic entities.

At the present stage I suggest that we can express our knowledge of the variability of reactive strength in heterozygotes and homozygotes in the accompanying figure, in which the homozygotes are given just one half of the variance of the heterozygotes, as would be the case if there were a number of allelic positive genes interacting without dominance in respect of strength of reaction, and in such a way that the difference in titre between two homozygotes was the same as that between the corresponding heterozygotes. Whatever may be the interpretation, however, the diagram will serve to illustrate

DISTRIBUTION INTO PHENOTYPIC CLASSES
OF HOMOZYGOTES (PP)
AND HETEROZYGOTES (Pp)



the variability of the two genotypes in relation to the boundaries dividing Strong from Medium, and Medium from Weak, the considerable overlap between their ranges, and the improbability, in view of this variability, of any distinct bimodality or multimodality being recognisable.

An important fact antagonistic to the existence of multiple alleles is the failure of absorption to indicate any qualitative difference between Strong and Weak reactors. This is in contrast to such cases as A_1 and A_2, or to the quasi-alleles of the Rhesus system.

6. SUMMARY

An analysis of Henningsen's family data, in which parents are classified as Strong, Medium and Weak reactors to anti-*P* serum shows that these three phenotypic classes contain very unequal proportions of heterozygotes.

Subject to errors of random sampling, the proportions are estimated to be

Strong	. . .	33·597	per cent. heterozygous
Medium	. . .	70·162	,, ,,
Weak	. . .	100·000	,, ,,

The total number of homozygotes estimated in this way, 123·9, agrees closely with the number 122·6, estimated from the proportion of Negative parents.

Of the total number enumerated it appears that the homozygotes are about equally divided between the Strong and Medium phenotypes; while of the heterozygotes about 14 per cent. are Strong, 67 per cent. Medium, and 19 per cent. Weak (see figure).

Homozygosity is therefore a well-established cause of the variation of reactive strength. As to the residual causes, it would appear premature yet to infer even that these are of genetic origin, still less that they can be ascribed to a series of recognisable alleles at the *P* locus.

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THE LINKAGE OF *POLYDACTYLY* WITH *LEADEN* IN THE HOUSE-MOUSE

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1. THE FACTOR *py*

THE existence of *polydactyly* as a recognisable Mendelian recessive in the house mouse was established by the work of S. B. Holt, who published decisive evidence in 1945 (1). In the following year (2) Holt and Wright were able to show that the same factor was present in the *fidget* stock in which polydactyly was observed by Grüneberg (5). It follows from Holt's work that in most of the occurrences of polydactyly studied in the literature, the situation has been much obscured by suppressors of varying intensity, so that no single-factor segregation has been observed, and that clear results will only be obtained by the use of stocks in which such suppressors have been largely eliminated. Somewhat more than 10 per cent. of suppression was, however, still present when Holt was obliged to relinquish this work.

Towards the end of 1948, I took over the care of the *polydactyly* stock (H) remaining in this department, which was at that time breeding about five in six polydactylous. The stock responded easily to selection, and from the following year I have had a closed stock in which polydactyly has invariably been manifest, as shown by over 500 mice bred in ten generations. The original stock H was, therefore, segregating in not many, perhaps only one suppressor. Outcrosses to other stocks have almost invariably shown evidence of one or more suppressors, sometimes capable of suppressing manifestation in as many as two-thirds of the mice recessive for the polydactyly factor (*py*) though usually less effective than this. The evidence for linkage between *py* and *ln* was thus somewhat obscured in the first matings in which it appeared, but by the end of 1949 it was possible (3) to report unmistakable linkage with recombination fraction of 20-30 per cent. in males. To the new linkage group so formed the number XIII was provisionally assigned. In reply to my information, Dr Snell at Bar Harbor informed me that his department had found *ln* to be weakly linked with *fuzzy*, *fz*, and strongly to *Splotch*, *Sp*, which he thought at that time to be linked with *Sd* (in Linkage Group V). It is now agreed that *Splotch* and *leaden* also belong to Linkage-Group XIII.

2. LINKAGE DATA

Stocks segregating in the factors of Linkage-Group XIII have now been established in this department. Since misconceptions appear still to be current as to the simplicity of the inheritance of

polydactyly in suitably prepared stocks (*e.g.* (4) Chase, 1951), it may be timely to put on record some of the linkage tests giving two-factor data for *polydactyly* and *leaden*.

The first mating giving clear single-factor segregation, with good though not perfect manifestation was put up in 1949, using a male doubly heterozygous in coupling, and gave 92 mice, which were classified in four classes as follows :—

TABLE 1

Males in coupling

	+	*poly*	*leaden*	*poly leaden*	Total
P 225 .	34	10	15	33	92

The crossover classes are about 27 per cent., and very significantly less than one-half. Two other matings of the same male later gave concordant results, as follows :—

P 325 .	15	5	12	15	47
P 326 .	13	4	4	13	34
Total .	62	19	31	61	173

In each case the double recessive was of the Élite polydactylous stock ; none the less it will be seen that the two crossover classes are sufficiently unequal to suggest either lower viability, or imperfect manifestation of polydactylous mice in these matings. Six confirmatory matings were made with males in coupling derived from the matings set out above ; these were :—

TABLE 1 (*concluded*)

	+	*poly*	*leaden*	*poly leaden*	Total
P 289 .	25	6	8	22	61
P 332 .	29	5	9	27	70
P 342 .	21	8	7	9	45
P 343 .	9	4	6	13	32
P 344 .	26	4	8	20	58
P 345 .	4	1	1	1	7
All C♂ .	176	47	70	153	446

I have plenty of evidence of occasional failure of manifestation, and little of any difference in viability. On the supposition of imperfect manifestation the simplest mode of calculation proceeds as follows :—

		Variance
47/(176+47) =	21·076 per cent.	7·459 (per cent.)^2
153/(153+70) =	68·610 ,,	9·658 (,,)^2
Manifestation	89·686 ,,	17·127 (,,)^2
Recombination	21·076/89·686 = 23·500 per cent.	
Sampling variance		6·090 (per cent.)^2

giving estimates of 89·7 per cent. manifestation, and 23·500 per cent. recombination. With these values the data are exceedingly closely

fitted, with χ^2 actually zero, thus giving no indication of disturbance due to unequal viability. The method of estimation used above was given by Bailey (7) in 1950. I have, however, modified his estimates of sampling variance.

In parallel with these nine matings of males doubly heterozygous in coupling, eleven such matings were made with females. These are given in table 2 :—

TABLE 2

Females in coupling

	+	*poly*	*leaden*	*poly leaden*	Total
P 301 .	22	11	13	10	56
P 306 .	30	10	15	20	75
P 322 .	12	9	7	19	47
P 323 .	28	13	13	17	71
P 347 .	5	5	4	11	25
P 388 .	7	4	4	4	19
P 389 .	7	3	5	6	21
P 390 .	7	2	10	10	29
P 392 .	11	7	4	8	30
P 399 .	10	5	7	7	29
P 400 .	10	3	10	6	29
All C♀ .	149	72	92	118	431

With the same calculations as for table 1, we find

		Variance
72/221	= 32·579 per cent.	9·939 (per cent.)^2
118/210	= 56·190 „	11·722 („)^2
Manifestation	88·769 „	21·661 („)^2

Recombination 36·701 per cent.
Sampling variance 7·055 (per cent.)^2

The fitting is again close, with $\chi^2 = 0{\cdot}272$ for one degree of freedom. The recombination fraction for females is remarkably larger than that for males, a circumstance which gives special interest to the verification of the values by matings in repulsion. The percentage manifestation is nearly the same, as might have been expected using males and females of the same parentage.

Eight matings using males in repulsion were obtained soon after the coupling series, but it is only recently that I have had results from females in repulsion. These two batches, therefore, are less closely related than those in coupling. It will be observed that the most recent lot has apparently perfect manifestation, as must occur sooner or later, save on the view that the gene *Py* is not an ordinary normal allelomorph. There has never been any evidence in favour of this possibility. In spite of all suggestions to the contrary, the gene *py* seems to be quite simply recessive.

The male repulsion series is shown in table 3 :—

TABLE 3

Males in repulsion

	+	*poly*	*leaden*	*poly leaden*	Total
P 364 .	8	8	22	6	44
P 382 .	12	8	11	5	36
P 383 .	4	16	23	4	47
P 384 .	11	23	21	6	61
P 385 .	19	24	28	2	73
P 461 .	2	0	2	0	4
P 462 .	1	4	2	0	7
P 463 .	1	6	7	1	15
All R♂ .	58	89	116	24	287

		Variance
89/147	= 60·544 per cent.	16·251 (per cent.)^2
24/140	= 17·143 ,,	10·146 (,,)^2
Manifestation	77·687 ,,	26·397 (,,)^2
Recombination	22·067 per cent.	
Sampling variance	11·522 (per cent.)^2	

The manifestation is here the worst of the series, which accounts partly for the larger variance. The difference in males between coupling and repulsion is 1·433 per cent. with a standard error about 4·2. There is thus full agreement between coupling and repulsion.

The repulsion series for females is given in table 4.

TABLE 4

Females in repulsion

	+	*poly*	*leaden*	*poly leaden*	Total
P 363 .	8	19	12	6	45
P 539 .	17	19	22	19	77
P 586 .	14	21	20	14	69
P 639, 791 .	11	13	13	14	51
P 653 .	20	17	14	12	63
P 665 .	11	18	14	9	52
P 672 .	17	25	20	16	78
All R♀ .	98	132	115	90	435

		Variance
132/230	= 57·391 per cent.	10·632 (per cent.)^2
90/205	= 43·902 ,,	12·014 (,,)^2
Manifestation	101·293 ,,	22·646 (,,)^2
Recombination	43·218 per cent.	
Sampling variance	5·641 (per cent.)^2	

The difference between coupling and repulsion in females is 5·274 per cent., with a standard error 3·87 per cent. Like the difference for males it is not significant, though that for females exceeds its standard error.

3. SUMMARY

The four tests are summarised in table 5 :—

TABLE 5

Summary of two-point linkage tests with py *and* ln

Sex	Phase	Number of mice	Manifestation per cent.	Recombination fraction per cent.	Standard Error
♀♀	Coupling . .	431	89	36·7	2·60
♀♀	Repulsion . .	435	100	43·2	2·38
♂♂	Coupling . .	446	90	23·5	2·47
♂♂	Repulsion . .	287	78	22·1	3·39
		1599			

In view of the agreement between coupling and repulsion data in each sex, we may calculate weighted means for the recombination fractions, namely

Females . . 40·3 per cent ±1·77
Males . . 23·0 „ ±2·00

Using Kosambi's relationship the map distance in females is estimated to be 55·8 cM, while that for males is only 24·9 cM. There would seem to be about half a chiasma difference between the two sexes in this portion of the strand alone.

It has taken some time to obtain four-point data in this chromosome with equally clear segregation. However, I hope soon to be able to set out the position more fully. The loose linkage between *fz* and *ln* has been fully confirmed, both sexes giving near to 40 per cent., with no very striking sex difference. *Leaden* and *Splotch* lie between *fuzzy* and *polydactyly*. The order given by Grüneberg (1952, (6), p. 479) namely *ln-Sp-fz-py* seems to be based on guesswork.

The four markers available in the thirteenth chromosome serve to map a greater map distance than is yet available in any other linkage group.

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A GENETICAL SYSTEM ADMITTING OF TWO DISTINCT STABLE EQUILIBRIA UNDER NATURAL SELECTION

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IT has long been known that in a population where different genotypes possess different selective advantages, it is possible for balanced polymorphism to exist. That is to say there is an equilibrium between the proportions of different genotypes, which is *stable* under random mating and differential viability and fertility. I do not know, however, whether any case has been recognised in nature or discussed theoretically in which it is possible for *two* distinct non-trivial stable equilibria to exist. (A trivial equilibrium is an extreme case when, for instance, some genes or genotypes are unrepresented in the population, and is of little interest.) It may therefore be of some theoretical interest to construct a genetical system admitting of two distinct stable states of balanced polymorphism.

Analogy with electrical and mechanical oscillating systems suggests that the necessary degree of complexity may be achieved by a system composed of two "coupled" sub-systems, possessing sufficiently unlike properties. Now the random mating of the sexes can be regarded as an interaction between two sub-populations. It is therefore natural to enquire whether a population in which the same genotypes have different viabilities in the two sexes is one admitting of a multiplicity of distinct equilibria. This expectation is verified. It is easy to specify a theoretical population involving three genotypes AA, A*a* and *aa* with selective advantages different within and between sexes, which has three equilibria, of which two are stable and the third unstable. For example with the scheme of viabilities

	AA	A*a*	*aa*
Females . . .	0·50	1·00	0·50
Males	2·15	1·00	2·15

we obtain three equilibria characterised as follows for gene ratios in the two sexes and for stability.

Equilibrium state	Gene ratio (A : *a*)		Character
	In females	In males	
I	0·582	0·339	Stable
II	1·000	1·000	Unstable
III	1·718	2·951	Stable

I give herewith a brief discussion of systems of this type. It is seen that they may possess

(i) no non-trivial equilibrium state, or
(ii) a unique non-trivial equilibrium which may or may not be stable, or
(iii) three non-trivial equilibria, of which as many as two may be stable, the third being unstable.

All the possibilities relating to the case of three equilibria, and the necessary conditions on the viabilities have not been exhaustively explored numerically, but their complete examination would present no great difficulty. The analysis suggests that a necessary condition for the existence of three equilibria is that in at least one sex, at least one homozygote must be at an advantage relative to the heterozygote. It suggests further that the difference in viability between homozygotes and the heterozygote is required to be in opposite senses in the two sexes.

Assume random mating and the gene frequencies

	A	*a*	Ratio
Females . . .	p_1	q_1	$u_1 = p_1/q_1$
Males	p_2	q_2	$u_2 = p_2/q_2$

together with parameters to express selective advantage as follows

	AA	A*a*	*aa*
Females . . .	$1-S_1$	1	$1-s_1$
Males	$1-S_2$	1	$1-s_1$

Then the genotypic proportions at an assigned phase in the life cycle are

	AA	A*a*	*aa*
Females . . .	$(1-S_1)p_1p_2$	$p_1q_2+p_2q_1$	$(1-s_1)q_1q_2$
Males	$(1-S_2)p_1p_2$	$p_1q_2+p_2q_1$	$(1-s_2)q_1q_2$

Thus in the next generation

$$u_1' = \frac{(1-S_1)u_1u_2+\frac{1}{2}(u_1+u_2)}{(1-s_1)+\frac{1}{2}(u_1+u_2)}$$

$$u_2' = \frac{(1-S_2)u_1u_2+\frac{1}{2}(u_1+u_2)}{(1-s_2)+\frac{1}{2}(u_1+u_2)}$$

In equilibrium $u_1' = u_1$, $u_2' = u_2$. Setting $t = u_2/u_1$ it is found that the equilibrium ratios are given by

$$u_1 = \frac{t-c_1}{1-C_1 t}, \qquad u_2 = \frac{c_2 t - 1}{C_2 t - t^2} \quad . \quad . \quad . \quad (1)$$

where $c_1 = 1-2s_1$ $\quad c_2 = 1-2s_2$

$C_1 = 1-2S_1$ $\quad C_2 = 1-2S_2$

and t satisfies the cubic equation

$$f(t) = t^3 - 3\alpha t^2 + 3\beta t - 1 = 0$$

with

$$\alpha = \tfrac{1}{3}(C_1 c_2 + c_1 + C_2), \ \beta = \tfrac{1}{3}(C_2 c_1 + c_2 + C_1)$$

Using the facts that $f(0) = 1$, and that $f(t) \to \infty$ as $t \to \infty$, and considering maxima and minima of $f(t)$ it is found that $f(t) = 0$ has a unique positive real root, unless the following conditions are satisfied simultaneously :—

$$\left.\begin{array}{ll} & \alpha > 0, \quad \alpha^2 > \beta > 0, \\ \text{and} & 4\alpha^3 + 4\beta^3 - 3\alpha^2\beta^2 - 6\alpha\beta + 1 < 0 \end{array}\right\} \quad . \quad . \quad . \quad (2)$$

When these conditions are fulfilled there are three distinct real positive values, t_1, t_2, t_3 of t satisfying $f(t) = 0$. If also u_1 when calculated by (1) is positive for each of these values of t, then there are three distinct non-trivial equilibria. This latter requirement can be expressed by saying that t_1, t_2 and t_3 must lie within the interval whose termini are $t = c_1$, $t = 1/C_1$.

Condition (2) may be written in the form

$$\phi(\beta) = \beta^3 - \tfrac{3}{4}\alpha^2\beta^2 - \tfrac{3}{2}\alpha\beta + (\tfrac{1}{4} + \alpha^3) < 0.$$

For given α and variable β it is seen that $\phi(\beta)$ has a minimum value

$$m = -2(\tfrac{1}{16}\alpha^4 + \tfrac{1}{2}\alpha)^{\frac{3}{2}} + 1 + \tfrac{5}{8}\alpha^3 - \tfrac{1}{32}\alpha^6$$

achieved when

$$\beta = \beta_m = \tfrac{1}{4}\alpha^2 + \sqrt{\tfrac{1}{16}\alpha^2 + \tfrac{1}{2}\alpha}.$$

The table of values of m and β_m shows that for all values of α in excess of α_0 (where α_0 is about 1·5), it is possible to find a range of values of β in the neighbourhood of β_m for which all the conditions for three equilibria are satisfied.

There is however a second continuum of α, β values satisfying the conditions. For taking $\beta = \alpha$ we see that the equation

$$t^3 - 3\alpha t + 3\alpha t - 1 = 0$$

has the roots

$$t_1 = \tfrac{1}{2}(k - \sqrt{k^2-4}), \quad t_2 = 1, \quad t_3 = \tfrac{1}{2}(k + \sqrt{k^2-4})$$

where $k = 3\alpha - 1$. Thus there are three equilibria provided that

$$3\alpha - 1 = k > 2,$$

i.e. provided that $\alpha > 1$. The same applies for all values of α greater than unity, and for values of β sufficiently close to α. It appears therefore that there are two distinct viability ranges for which the system has three equilibria.

TABLE

α	ϕ_m	β_m	α^2
1·0	0·00000	1·000	1·00
1·2	0·18784	1·214	1·44
1·4	0·21827	1·424	1·96
1·5	0·00013	1·595	2·25
1·6	−0·05549	1·740	2·56
1·8	−0·31425	2·057	3·24
2·0	−1·90684	2·414	4·00
∞	−∞	∞	∞

It is informative to consider the special case when in each sex the homozygotes have equal viabilities. Take therefore $S_1 = s_1$, $S_2 = s_2$. Then

$$\alpha = 1 + \tfrac{4}{3}(s_1 s_2 - s_1 - s_2),$$

so that

$$(1-s_1)(1-s_2) = 1 + \tfrac{3}{4}(\alpha - 1).$$

Since $\alpha > 1$ is a necessary condition for three equilibria we get as a further necessary condition

$$(1-s_1)(1-s_2) \geqslant 1.$$

Consequently at least one of the homozygous viabilities $1-s_1$, $1-s_2$ exceeds unity.

The more specialised case in which $S_1 = s_1 = S_2 = s_2$, gives all viabilities equal as between sexes, a situation which admits of at most one equilibrium. This suggests that for three equilibria to exist, the difference in viability between homozygotes and heterozygotes is required to be in opposite senses in the two sexes.

Returning to the general case, we note the following procedure for investigating the stability of any equilibrium state. In place of u_1 and u_2, write $u_1 + x_1$, $u_2 + x_2$ giving u_1 and u_2 their equilibrium values. Then neglecting quadratic terms in x_1 and x_2 we get the approximate recurrence relations

$$x_1' = b_{11}x_1 + b_{12}x_2, \qquad x_2' = b_{21}x_1 + b_{22}x_2,$$

where

$$b_{ij} = u_i \frac{\partial}{\partial u_j}(\log u_i') \quad (i, j = 1, 2)$$

and u_1, u_2 are put equal to equilibrium values after differentiation. The equations in x_1, x_2 have solutions of the form

$$x_{1n} = B_{11}\lambda_1^n + B_{12}\lambda_2^n, \quad x_{2n} = B_{21}\lambda_1^n + B_{22}\lambda_2^n$$

where λ_1, λ_2 are the latent roots of the matrix (b_{ij}). Consequently the equilibrium state is stable or unstable according as to whether both λ_1, λ_2 are or are not less than unity.

The example given in the introduction was constructed by taking $\alpha = 1{\cdot}1 = \beta$, so that the appropriate roots were

$$t_1 = 0{\cdot}582109, \quad t_2 = 1{\cdot}0, \quad t_3 = 1{\cdot}717{,}891.$$

We require as subsidiary conditions either

(i) $1-2s_1 = c_1 < 0{\cdot}582$ and $1-2S_1 = C_1 < 0{\cdot}582$

corresponding to homozygous viabilities $1-s_1$, $1-S_1$ less than 79 per cent., or

(ii) $1-2s_1 = c_1 > 1{\cdot}718$ and $1-2S_1 = 2S_1 = C_1 > 1{\cdot}718$

corresponding to homozygous viabilities greater than 136 per cent. For simplicity we take an extreme case in which $c_1 = C_2 = 0$, (*i.e.* the homozygotes among females have viabilities of 50 per cent. only, while in the males their viabilities are 215 per cent.) and obtain three equilibria as described, the stability roots being :—

I. 0·9617, 0·0383 ; II. 0, 1·0159 ; III. 0·7277, 0·1283.

As a second example we may take the table of viabilities

	AA	A*a*	*aa*
Females . . .	0·5	1·0	0·5
Males	4·1	1·0	3·5

for which $\alpha = 2$ and $\beta = 2{\cdot}4$, obtaining equilibria as follows :—

State	Gene ratio (A : *a*)		Character	Stability roots
	In females	In males		
I	0·16	0·026	Stable	0·91 , 0·07
II	1·42	2·00	Unstable	1·02 , −0·14
III	4·42	19·57	Stable	0·92 , 0·11

Both examples illustrate the case when there are two equilibria, each characterised by a rather large disparity of the gene ratios in the two sexes. If such differences in gene ratio were to be observed in an ecological situation, they would be suggestive of the existence of the peculiar kind of balance that has been examined.

The present discussion clearly does not exclude the possibility of cases in which there are three non-trivial equilibria of which only

one (presumably the intermediate one) is stable. An answer to this question would be of interest, and could take one of two forms. It may be possible to demonstrate algebraically that these cases do not exist. On the other hand it may be possible to construct an illustrative numerical example.

In the case where one allele A is lethal in both sexes when in the homozygous condition AA it is easy to see that there are at most two non-trivial equilibria of which only one is stable.

The writer has profited from helpful discussions with Walter Peters at present working in this department, whose field observations suggested this problem.

SUMMARY

It is shown that different viabilities of genotypes in the two sexes may lead to either of two stable equilibrium states being realised in a population under random mating.

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SUPER-RECOMBINATION IN THE SEX CHROMOSOME OF THE MOUSE

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1. INTRODUCTION

THE occurrence of recombination fractions significantly in excess of 50 per cent. may conveniently be named *super-recombination*. A case of this kind was reported (1) by Mrs M. E. Wallace (M. E. Wright) in 1947. She found that in the house mouse the two factors wv_2 (wavy$_2$) and sh_2 (shaker$_2$) showed respectively with *sex* the recombination values 56·07 and 56·73 per cent., but only 31·06 per cent. recombination with one another. At the same time a theoretical explanation (2) (principally due to Sir Ronald Fisher) was put forward which showed that these results could be accounted for on the basis of genetical interference. The theoretical treatment was based on the following assumptions.

(*a*) An interference metric u exists on which the intercept lengths formed on a strand by consecutive exchange points are distributed independently in accordance with a frequency distribution

$$dp = f(u)du.$$

(*b*) The interference function $f(u)$ approximates to

$$f(u) = \frac{d}{du}(-\operatorname{sech} \tfrac{1}{2}\pi u).$$

(*c*) There is negligible interference across the centromere.

These assumptions are general in character and have been maintained in later work (3-8), except for a slight modification of the form of $f(u)$. At the time a further assumption was made relative to the situation in the sex chromosome of the mouse, namely that

(*d*) the centromere is remote from the sex-determining portion.

In the later work on this theory (loc. cit.) it was found possible to take account of the fact that the arms of chromosomes are not infinitely long in comparison with the mean intercept length but have termini at finite distances. I have given (4) a brief account of this part of the theory, and a more extended account will be published elsewhere. In 1948 I carried out a further discussion of Wright's results in order to consider them with reference to finite arm length. The work was much facilitated by the fact that it had proved possible to replace the form for $f(u)$ quoted above by the simpler one $4ue^{-2u}$, which has been found to give predictions in agreement with Kosambi's theory (of proved utility (9-11)) and with data on interference in *Drosophila melanogaster* (8, 12). This discussion was not published at

the time, though it appeared as part of a Ph.D. dissertation (12). I think, however, that now it may be of some interest since Carter and Robertson in a recent paper (13) have drawn attention again to Wright's data as an apparently well substantiated case exhibiting super recombination due to loose linkage and genetical interference. Elsewhere (10) I have made criticisms of Carter and Robertson's particular modification of recombination theory, and in this note wish only to consider those of their theses which are relevant to the interpretation of Wright's data. They say that when all chiasma pairs involve four strands, and chiasma interference is absent, then the maximum recombination fraction is 53·34 per cent. This is equivalent to the statement that with the function $4ue^{-2u}$ recombination cannot exceed 53·34 per cent. This is indeed true for an infinitely long chromosome arm, which is the only model studied by Carter and Robertson, but is not true when account is taken of arm lengths that though long are less than infinite. It will be seen from the present discussion that recombinations of the order of 60 per cent. are possible with the function $4ue^{-2u}$ when allowance is made for the arm terminus.

There is a second point, also relevant, which merits some examination. Carter and Robertson correctly point out that super-recombination requires some degree of chromatid interference, and is not incompatible with there being some degree of chiasma interference. However, they imply that the function $4ue^{-2u}$ is of limited applicability, its use precluding the assumption of any chiasma interference, and in particular is not competent to explain Wright's data. It is indeed true that this function applies exactly only when chiasma interference is absent and chromatid interference is complete. However, I showed in 1948 (12) that it applies to a good degree of approximation (which is all that is necessary in view of the relative imprecision of even the best genetical data) in a variety of other circumstances, *i.e.* with various degrees of incomplete chromatid interference allied with appropriate intensities of chiasma interference. Its use for practical purposes seems therefore to be admissible on ample theoretical grounds, quite apart from the empirical support given by Kosambi's formula (loc. cit) and data on *Drosophila melanogaster* (loc. cit.).

I find the following example particularly striking though it is only one of a complete sequence that can be constructed. Let us assume a degree of chiasma interference such that, relative to a genetical interference metric u, the *chiasma* intercept length is distributed as

$$dp = ue^{-u}du,$$

and suppose that chromatid interference operates in such a way that when a strand has been involved in a chiasma it has a probability of 1/3 (as opposed to 1/2) of being involved in the next chiasma. Then it will be found that the genetical interference function is

$$g(u) = 16e^{-4u}\left(\frac{1}{\sqrt{3}}\sinh\frac{4u}{\sqrt{3}} - u\right).$$

The mathematical form of $g(u)$ has indeed but a small resemblance to the more modest $f(u) = 4ue^{-2u}$ but tabulation shows that the two functions closely mimic one another over the range $(0 \leqslant u \leqslant 3)$ *i.e.* over about 275 cM of map distance. Table 1 gives their value together with the absolute discrepancy (error column) and the discrepancy as percentage of the value of $f(u)$. The error is trivial until u exceeds 3. Beyond this point it might indeed affect delicate phenomena such as super-recombination on arms longer than 275 cM. For shorter arms, however, the divergence at the tails is irrelevant, and the functions are to all intents and purposes the same.

TABLE 1

Metric u	Map length x cM	$f(u)$	$g(u)$	Error	Per cent. error
0	0	0	0	0	...
0·25	9	0·60653	0·60242	−0·00411	−0·68
0·50	28	0·73596	0·70483	−0·03113	−4·23
0·75	50	0·66939	0·66251	−0·00688	−1·02
1·00	75	0·54134	0·55101	0·00967	1·79
1·50	125	0·29872	0·30635	0·00763	2·55
2·00	175	0·14653	0·14655	0·00002	0·00
2·50	225	0·06738	0·06575	−0·00163	−2·42
3·00	275	0·02975	0·02873	−0·00102	−3·43
4·00	375	0·00336	0·00528	0·00192	57·14

In showing that the function $4ue^{-2u}$ could be regarded as having its genesis in an approximation to special models involving explicitly postulated mechanisms of chromatid and chiasma interference, I do not wish to imply that there is any warrant for putting forward such detailed models as effective descriptions of reality. I believe that the actual phenomena are in fact so complicated as to be outside the scope of manageable mathematical description. It seems much the more realist policy to regard genetical interference as a unitary phenomenon (which probably it is) described adequately by a specification of the exchange point distribution on any one of the meiotic strands. This self denying ordinance keeps us within the range of concepts capable of some verification from genetical observations, *i.e.* the breeding behaviour of organisms.

To sum up, we can say that use of $4ue^{-2u}$ involves us in no patent subservience to over-restricted models of crossing-over, nor in any patent conflict with theories of crossing-over. Its use is consistent with various postulated partitions of interference between chromatid and chiasms components. When finite arm length is taken into account it is capable of yielding values exceeding 53 per cent., should such values be required by experimental data of sufficient precision. These remarks apply with equal force to any close mimic of the function *e.g.* to

$$\frac{d}{du}(-\operatorname{sech} \tfrac{1}{2}\pi u).$$

2. ASSUMPTIONS REGARDING THE SEX CHROMOSOME

In the male no chiasmata are likely to occur in the differential segment. In the original discussion we therefore took P, the point of junction of the pairing segment and the differential segment, as the effective terminus of one arm of the sex-chromosome. Since there were no chiasmata in the differential segment beyond P we assumed that the exchange point E formed nearest to P was exempt from any interference originating between it and P or beyond P. Thus the probability distribution of u, the metrical distance of this exchange point from P, was chosen to be a function of Poisson type, namely

$$\frac{d}{du}(-e^{-\frac{1}{2}\pi u}),$$

which is the limiting form of the tail of the distribution

$$\frac{d}{du}(-\operatorname{sech} \tfrac{1}{2}\pi u).$$

The centromere was assumed to be effectively at an infinite distance from P, so that the only repressive influences inhibiting the formation of exchange points further from P than E were exerted by established exchange points and represented by the interference function

$$\frac{d}{du}(-\operatorname{sech} \tfrac{1}{2}\pi u).$$

The map distance and recombination between P and a locus at metrical distance t from P were then tabulated numerically.

The assumptions about the terminus P were in fact equivalent to those used by the writer (4) in an analysis appropriate to arms of finite length. The numerical study may therefore be repeated using the function $4ue^{-2u}$ and the established formula (loc. cit.).

3. CENTROMERE ASSUMED REMOTE

Retaining the hypothesis that the arm is of very great length and the centromere very remote from P, let $x(t)$ and $y(t)$ be the map distance and recombination between the terminus and a locus at metrical distance t from it. Then, with the function $4ue^{-2u}$, we have

$$x(t) = t+\tfrac{1}{4}-\tfrac{1}{4}e^{-4t}$$
$$y(t) = \tfrac{1}{2}-\tfrac{1}{2}e^{-2t}(\cos 2t-\sin 2t).$$

These functions are tabulated in table 2, along with the corresponding figures for the function

$$\frac{d}{du}\left(-\operatorname{sech} \frac{\pi u}{2}\right)$$

transcribed from the earlier paper (2).

The new function gives a higher maximum for y than does the earlier one. The new value is 60·394 per cent., *i.e.* $\frac{1}{2}(1+e^{-\frac{1}{2}\pi})$, as opposed to 55·8 per cent. The points where y has values 56 and 57 per cent. are more than 60 cM apart, a fact which somewhat strains agreement with the known separation of wv_2 and sh_2, of the order 35-40 cM only.

TABLE 2

Recombination and map distance between end of pairing segment and locus at metrical distance t *when the centromere is infinitely remote*

t	Old function		New function	
	$x(t)$ cM	$y(t)$ per cent.	$x(t)$ cM	$y(t)$ per cent
0	0	0	0	0
0·1	14·598	14·474	18·242	18·013
0·2	27·430	26·496	33·767	32·182
0·3	39·069	36·125	47·470	43·082
0·4	49·955	43·497	59·953	50·464
0·5	60·399	48·831	71·616	55·540
0·6	70·601	52·405	82·707	58·579
0·7	80·687	54·535	93·480	60·055
0·8	90·727	55·734	103·981	60·361
0·9	100·756	55·734	114·317	59·927
1·0	110·789	55·275	124·542	58·969
1·1	120·832	54·688	134·693	57·740
1·2	130·886	53·846	144·794	56·409
1·3	...	...	154·862	55·097
1·4	...	...	164·908	53·884

Thus the quantitative difference between the old and the new functions, while very slight, shows up in the rather delicate phenomenon of super-recombination. The functions are such close mimics of one another that their predictions in respect of the short-range properties of linkage groups are not readily distinguishable. They are similarly equally compatible with *a priori* theoretical requirements as considered above. The discrepancy in the present application does however show how unwise it would be to dogmatise about numerical magnitudes in the more delicate long-range phenomena of which super-recombination is one.

4. ADMISSABLE HYPOTHESES WHEN THE CENTROMERE IS ASSUMED LESS REMOTE

The values of the recombinations of wv_2 and sh_2 with sex require both loci to be fairly remote from the terminus (90 cM or more), unless the interference is much in excess of the Kosambi level *i.e.* that associated with $4ue^{-2u}$, (*cf.* Owen, 1951, (6)). With interference of the Kosambi order of magnitude, wv_2 and sh_2 must both be 90 cM

or more from the terminus but the observed values are compatible with the centromere being located either between or beyond them.

Table 3 shows the maximum recombination value with the terminus which a locus on arms of various lengths may attain, when the interference function is $4ue^{-2u}$. The recombination between

TABLE 3

Maximum recombination with terminus (y_m) *and recombination between terminus and centromere* (y_o) *on arm of metrical length T*

T	Arm length cM	y_m per cent.	y_o per cent.
0·785	72·033	50·000	50·000
0·800	73·734	50·582	50·566
0·900	85·213	53·569	53·656
1·000	96·403	55·892	55·531
1·100	107·331	57·361	56·442
1·200	118·040	58·356	56·635
1·300	128·574	59·027	56·330
1·400	138·968	59·479	55·710
1·500	149·258	59·782	54·917
1·600	159·469	59·986	54·062
1·700	169·621	60·123	53·223
1·800	179·732	60·215	52·245
1·900	189·810	60·277	51·769
2·000	199·866	60·318	51·197
∞	∞	60·394	50·000

centromere and terminus is also indicated. For arms of the order of 200 cM the maximum value y_m is close to the value achieved on the infinite arm. This will be equally true when the function is

$$\frac{d}{du}(-\text{sech } \pi u/2).$$

Hence the original treatment will apply to a good order of approximation if the arm is of this length.

To ascertain what arm length (T in metrical units) is compatible with the hypothesis $f(u) = 4ue^{-2u}$, the course of the recombination fraction has been plotted for T = 1·40 and T = 1·00. In the former case the centromere would lie beyond wv_2 and sh_2 at 138·97 cM from the end of the differential segment. x and y are shown in table 4. Close agreement with Wright's data is not obtained. The maximum of y is too large on this theory, while wv_2 and sh_2 would be required to be about 50 cM apart.

Table 5 shows x and y calculated on the hypothesis that the centromere lies at T = 1·00, and at 96·4 cM from the differential segment. It is assumed that there is no interference across the

centromere. The agreement is about as good as that obtained in the original treatment.

The last hypothesis to be examined is that the centromere lies between the pairing segment and the factors wv_2, sh_2. This is easily

TABLE 4

Map length and recombination over a terminal segment or an arm of metrical length 1·40

t	$x(t)$ cM	$y(t)$ per cent.
0	0	0
0·1	18·09	17·865
0·2	33·45	31·887
0·3	46·97	42·336
0·4	59·19	49·882
0·5	70·58	54·827
0·6	81·28	57·756
0·7	91·46	59·155
0·8	100·89	59·461
0·9	110·29	59·058
1·0	118·78	58·265
1·1	126·38	57·344
1·2	132·72	56·511
1·3	137·21	55·925
1·4	138·97	55·710

TABLE 5

Map distance from and recombination with terminus when centromere is at 96·64 cM from terminus

t	$x(t)$ cM	$y(t)$ per cent.
0	0	0
0·1	17·513	17·293
0·2	32·249	30·744
0·3	45·033	40·697
0·4	56·373	47·625
0·5	66·556	52·062
0·6	75·654	54·560
0·7	83·595	55·660
0·8	90·091	55·876
0·9	94·635	55·686
1·0	96·403	55·531
1·1	98·170	53·618
1·2	102·715	52·130
1·3	109·211	51·029
1·4	117·152	50·263

verified to be quite incompatible with interference at the Kosambi level. Recombinations of the right order could only be obtained with interference of much greater ferocity, with a mean intensity of the order 0·8 (*cf.* Owen, 1949 (3)).

To summarise, it may be said that Wright's data are compatible with interference of Kosambi order if either

(*a*) the arm length is of the order of 200 cM, with the centromere lying beyond wv_2 and sh_2 (the old interference function giving a better fit than the new), or

(*b*) the centromere is situated between these factors and distant about 90-100 cM from the differential segment (the new interference function being used).

The data are definitely incompatible with the assumption that the centromere is near to the differential segment unless it is the case either that interference is operating with exceptional severity or that there is strong interference across the centromere.

5. SUMMARY

It is shown that contrary to the supposition of Carter and Robertson, the functions used to represent genetical interference are compatible with four strand crossing-over without complete chromatid interference and with some chiasma interference. It is also made clear that when account of the chromosome termini is taken these functions yield recombination values in excess of 53·34 per cent. and are competent to explain Wright's data on wv_2, sh_2 and sex in the house mouse. It is shown that these data are consistent with a centromere at a distance of the order of 200 cM from the differential segment, with wv_2 and sh_2 lying between the centromere and the pairing segment, or with the centromere lying between these factors and at about 100 cM from the differential segment.

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STATISTICAL MODELS IN BIOMETRICAL GENETICS

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1. INTRODUCTION

THE statistical models belonging to the analysis of discontinuous variation in genetics have an elegance and exactness which are rare in the field of applied statistics. This is partly due to the qualitative nature of the characters usually investigated and partly to the random processes inherent in meiosis and fertilisation ; both these properties of the experimental material make it possible to specify the hypothesis to be tested with great accuracy. The contrast between this state of affairs and that found when continuous variation obtains is indeed striking. The assumption that continuous variation represents the combined effect of polygenic inheritance and a blurring environmental overlay, though necessary as a basic postulate, is too vague to allow analysis to proceed very far. A further difficulty lies in the fact that experimental data on continuous variation, at least as obtained by present methods, do not suggest a detailed hypothetical structure which can be tested in future work. The hypotheses capable of being tested at present are relatively imprecise, and it must be expected, therefore, that the prediction value of analyses of continuous variation will be correspondingly less than that found in discontinuous variation. The analyses themselves will be less efficient, in the Fisherian sense, for the basic reason that the lack of plausible *a priori* structures for polygenic variation makes the construction of likelihood functions for sets of readings impossible, with the consequence that more or less inefficient *ad hoc* methods of analysis have to be used in default of anything better.

We shall consider in this paper the assumptions underlying the simpler models used in biometrical genetics and some of the statistical consequences of these models, with particular reference to the type of experiment in which the data relate to the descendants of a cross between two true-breeding lines. The discussion will be restricted to the analysis of first-order statistics (means) and second-order statistics (sums of squares and products) only.

2. GENOTYPIC AND PHENOTYPIC EFFECTS

The distinction between genotype and phenotype, that is, between genetic structure and its individual expression, is basic in genetics. In the analysis of continuously varying characters, it is usually said that we make the assumption that a measurement (x) can be represented as the sum of a component due to genotype (g) and a component

due to environment (e), *i.e.* $x = g+e$. It has been objected to this course in that the interaction between heredity cnd environment is so complex that its representation by a model such as $x = g+e$ is naive, even meaningless. It is worth while considering in more detail what meaning can be given to g and e in the above relation. It is clear that the idea of an ideal mean expression of a genotype is extremely vague. The combinations of environmental factors affecting development are practically infinite and there is no way in which we can weight the combinations in forming such a mean genotype. In any given experiment, however, the idea of randomisation can be used to define g. Consider an experiment in randomised blocks, in which each block contains an assemblage of plants of different genotypes, the numbers of each type being fixed beforehand. Under randomisation the plants of a given genotype in any block are distributed at random and give measurements $x_1, x_2, \ldots, x_k$, say, of some character. Writing $\bar{x} = \frac{1}{k}(x_1+x_2 \ldots +x_k)$ then $\bar{x}$ is a random sample of one from the randomisation population of all possible arrangements of the k plants in the block. Averaging over this population we may write $g = \mathrm{E}(\bar{x})$; and $e = x_i - g$. Two consequences of this definition may be noted. First, g as so defined is strictly local and must be expected to vary from experiment to experiment ; secondly, we do not assume that the population of residuals is fixed by the experiment independently of the actual distribution of the genotypes in the block. The restrictiveness in the above definition of g does not mean that no generalisation can be made from the experiment. For example, all variances and comparison of means are functions of *differences* of the g's and these may be expected to be more stable and so make possible a wider degree of generalisation. Even so, on general grounds we should expect that the differences of the g's will not be independent of the place and year of the experiment since the relative " fitness " of the different genotypes will be different under different external conditions.

The additional assumption that the residuals are independent of the distribution of the genotypes in a block greatly simplifies the analysis since this implies, among other things, that the " e " or environmental component of variance is independent of the genetic or " g " component, and hence in the expectation of all second-order statistics deriving from the same type of physical layout, the environmental component of variance is the same. This would still be true if the hypothetical populations of residuals of the various genotypes had the same variances without being necessarily identical, this being a slightly less restrictive assumption.

Assumptions about the structure of g

Consider a character affected by k loci. In general g will be some function of the alleles at all the loci, *i.e.* we may write

$g = g(\alpha_1, \alpha_2, \ldots, \alpha_k)$ where α_i, $i = 1, 2, \ldots, k$, represents the state of locus i in some genotype. The most obvious simplifying assumption here is that of independent action, which we may represent symbolically by $g(\alpha_1, \alpha_2, \ldots, \alpha_k) = g_1(\alpha_1) + g_2(\alpha_2) + \ldots + g_k(\alpha_k)$, so that the effect of each locus is independent of the state of the others.

Since such additivity is partly dependent on the scale of measurement, we are at liberty to adjust the scale to ensure at least average additivity, *provided that the equal-variance property of the residuals over the genotypes is also preserved.* Here we have a point of difference between the analysis of second-order statistics (as in biometrical genetics) and that of first-order statistics (as in, say, factorial manurial trials). In a factorial manurial trial, the absence of treatment interactions and the homogeneity of residual variances both simplify the analysis and interpretation but heterogeneity of residual variances does not, for example, bias the estimation of response slopes, although information may be lost. In biometrical genetics, additivity and the independence of g of e must *both* hold if the analysis is to proceed. This introduces a restriction on the characters which can be analysed with the present model ; how serious this restriction is remains to be seen.

For experiments on the generations following the crossing of two true-breeding strains, the following notation, developed by Fisher, Immer and Tedin (1932) and extended by Mather (1949) is convenient. For a gene pair *A-a* (multiple allelomorphs are excluded by the derivations of all the plants from two true-breeding lines), the values of g for **AA**, **Aa**, **aa**, measured as a deviation from the mid-parent value are d_a, h_a, $-d_a$ respectively. Given additivity, the value of g for any genotype is the sum of the appropriate $-d$'s, h's and $+d$'s. The expectation of the genetic portion of any second-order statistics can be expressed as a quadratic function of the d's and h's with coefficients depending on the recombination fractions and viability ratios of the different genes. When there is no differential viability, many (but not all) of the second-order statistics given by Mather are separable into two parts, one, denoted by D, depending only on the d's and the recombination fractions and the other, denoted by H, only on the h's and the recombination fractions.

3. THE ESTIMATION OF *D*, *H*, AND *E*

The experiments described by Mather consisted of blocks of plots, each plot containing an F_3 family, F_2 plants, F_1 or parent plants, etc. From each block second-order statistics are available, estimating the variance of F_2 plants, F_3 means, etc. The variance estimates include two measuring the non-heritable portion of the variance, one between plot means (taken from replicates of F_1 and parent plots within a block) and the other within plots (taken from the intra-plot variance of F_1 and parent plots). The expected values of the variance estimates are known linear functions of D, H and E, and D and H may be

heterogeneous due to linkage. There is a resemblance in the structure of this model to that used in " classical " least-squares analysis, where the expectations of certain observations are assumed to be known linear functions of some unknown parameters. There are, however, some differences too. In the least-squares analysis the " errors " in the observations (*i.e.* the differences from the expected values) have a variance matrix V say, which is assumed known and in almost all practical cases it is assumed that $V = \sigma^2 I$, where I is the unit matrix. Here, the variance of the errors is constant and the observations are uncorrelated. The arithmetic in this case is reasonably tractable, but is much more tedious for a general V.

Deviations of V from $\sigma^2 I$ can be divided conveniently into two kinds, (i) the deviation of the leading diagonal terms (*i.e.* the variances) from equality, and (ii) the deviations of the other terms (*i.e.* the covariances) from zero. There are several reasons why it is likely that the variance matrix of the second-order statistics in biometrical genetical experiments will deviate from the unit matrix. Deviations of the first type would certainly occur under the normal model, where a variance estimate x with expectation η and based on ν d.f. has a variance $2\eta^2/\nu$, which thus depends on both η and ν. Similar deviations are to be expected on the randomisation model. Deviations of the second kind will occur in the covariance of $V_{\overline{F3}}$ and $\bar{V}_{F3}$, and similar pairs. The correlation of the non-heritable components may be seen by considering E_1 and E_2. A uniform block will produce a small E_1 and E_2 and a variable block a large E_1 and E_2. We therefore expect a positive correlation between E_1 and E_2 as estimated from separate blocks. This is very marked in Mather and Philip's barley experiment (Mather, 1949) where the correlation is 0·9975, which, although based only on five pairs of observations, is nevertheless significant. Similar positive correlations are to be expected between V_{F2} and E_1, $V_{\overline{F3}}$ and E_2 for the same reason.

The effects of deviations from the assumed variance matrix in least-squares analysis are twofold, namely loss of efficiency in estimation and biasing of the standard errors. It should be noted that the estimates of D, H, etc. are *not* biased, but their sampling variances are inflated by the inefficient method of estimation. The bias in the standard errors is more serious because all significance tests are then unreliable.

The disturbing effects of the correlations mentioned above can be partly annulled by considering each block as a separate experiment with its own E_1 and E_2, these being now regarded as estimates of the randomisation variance within the block. In this way each block gives an estimate of D and H and standard errors can be obtained from the set of estimates by the usual methods. Until sufficient data are available to cast some light on the distribution of such estimates, this procedure must be regarded as a " large-sample " one.

Although this approach has the advantage that we avoid assump-

tions about the variance matrix of the original statistics and assume only that the estimates of D and H from the various blocks can be regarded as samples from a normal population (or, at least, one for which the Central Limit Theorem holds), there are still difficulties remaining. Certain types of correlation are not eliminated, among them being that between $V_{\overline{F3}}$ and $\bar{V}_{F3}$ due to the heritable part of the variance and that between E_1 and E_2. Evaluation of the former type in special cases is tedious but in the case of one gene and with normal residuals the correlation does not appear to exceed 0·2 in absolute value. The correlation between E_1 and E_2 is for the most part a consequence of the lack of a randomisation set *within* plots. One way out of this difficulty would be a complete randomisation of all plants in a block so that, *e.g.* F_1 plants would be found scattered over the block at random. Although such a complete randomisation might give rise to practical difficulties in some cases, it would have the analytical advantage in that there is now only one E occurring in the analysis and its contributions to the statistics, though not equal, are of known relative weight. It should also be noted that randomisation generates correlations (usually negative but not necessarily so) between sum of squares having no measurements in common, such as, *e.g.* V_{F2} and $V_{\overline{F3}}$. An extreme instance of this is provided by a variety trial in randomised blocks where no treatment differences exist. In this case the sum of the treatment and error sum of squares is a constant on the randomisation model so that their correlation is -1. In general, however, such correlations will be insignificant provided that there are a large number of plants in a block and that the plants contributing to the two sums of squares form only a small proportion of the whole.

Re-examination of Mather and Philip's Barley Experiment

This experiment, fully recorded and analysed by Mather (1949) (see particularly pp. 97-101), used as the variable a discriminant function compounded of ear width, total ear length, and length of the central six internodes, derived from previous data. The experiment comprised five blocks and each block provided statistics V_{F2}, $V_{\overline{F3}}$, $W_{F2/F3}$, $\bar{V}_{F3}$, E_1 and E_2. The analysis made in Mather's book follows the usual least-squares procedure and regards the separate E_1, E_2 as samples from a population. We shall now consider an alternative analysis following the approach considered in the previous section. Although a least-squares analysis will be used for each block, it is not suggested that this will give the most accurate estimates of D, H, and E, and the inverse c-matrix (see, *e.g.* Fisher (1948), pp. 156-164) will not be used to provide standard errors, which will be obtained from the sum of squares of the separate estimates from the five blocks. The estimates given by the method are unbiased as previously pointed out, and can be regarded as the best under the circumstances, bearing in mind that we have no prior information on the relative variances

and covariances of the second order statistics. It should be said in advance that, qualitatively speaking, the conclusions drawn from the analysis in no way differ from those of Mather, and the re-analysis is made simply to demonstrate the method employed.

In making the analysis, opportunity has been taken to introduce a slight refinement in putting the expectation of $V_{\overline{F3}}$ equal to $\frac{1}{2}D+\frac{1}{16}H+\sigma'^2+\frac{1}{n}(\frac{1}{4}D+\frac{1}{8}H+\sigma^2)$ where n is the harmonic mean of the number of plants contributing to each mean, and σ'^2 is defined as the variance *component* of plot means instead of the total variance of plot means. Thus (writing $\mathcal{E}$ for expectation)

$$\mathcal{E}(E_2) = \sigma'^2+\frac{\sigma^2}{n}$$

$$\mathcal{E}(E_1) = \sigma^2$$

σ^2 and σ'^2 have been introduced for the two non-heritable components of variance in order that E_1 and E_2 may be reserved for the estimates and not used also for the population parameters. In order to avoid the recalculation of inverse matrices, n has been taken as 10 throughout, though, owing to the loss of plants, this is not strictly true for each block.

Table 1 gives the values of the statistics for each block together with their expectations.

TABLE 1

Statistic	Block					Expectation
	A	B	C	D	E	
V_{F2}	9492·0	11540·9	9179·5	8673·7	9926·4	$\frac{1}{2}D+\frac{1}{4}H+\sigma^2$
$V_{\overline{F3}}$	6289·7	5838·6	5935·1	7148·8	6013·4	$\frac{1}{2}D+\frac{1}{16}H+\sigma'^2+\frac{1}{10}(G+\sigma^2)$
$W_{F2/F3}$	6934·6	6342·5	6742·5	7439·6	6696·8	$\frac{1}{2}D+\frac{1}{8}H$
$\bar{V}_{F3}$	4513·1	4532·5	4342·4	4323·1	3867·9	$G+\sigma^2$
E_1	1443·8	736·9	1433·1	1720·9	747·6	$\sigma'^2+\frac{1}{10}\sigma^2$
E_2	278·6	57·9	306·8	403·2	54·9	σ^2

G is the genetic portion of the variance within F_3 families and $G = \frac{1}{4}D'+\frac{1}{8}H'$. In the absence of linkage $D' = D$, $H' = H$. In the presence of linkage, $D' \neq D$, $H' \neq H$; D' and H' cannot be estimated separately in the absence of other statistics giving information about them.

Fitting one D, one H and separate E's to the data and putting $G = \frac{1}{4}D+\frac{1}{8}H$, we find from least squares

$$\hat{D} = 9602{\cdot}3, \quad \hat{H} = 15{,}270{\cdot}6, \quad E_{1A} = 840{\cdot}2 \quad E_{2A} = 106{\cdot}9$$
$$E_{1B} = 1294{\cdot}0, \quad E_{2B} = -274{\cdot}4, \quad E_{1C} = 675{\cdot}6, \quad E_{2C} = -39{\cdot}9$$
$$E_{1D} = 596{\cdot}5, \quad E_{2D} = 623{\cdot}1, \quad E_{1E} = 537{\cdot}9, \quad E_{2E} = -112{\cdot}9$$

(where $\hat{D}$ and $\hat{H}$ denote the estimates of D and H, and E_{1A}, E_{2A} are the estimates of E_1 and E_2 in block A, etc.).

The sum of squares of residuals is 10,526,166. Fitting one D, one H, one G, and separate E's we find

$$\begin{aligned} \hat{D} &= 9800{\cdot}3, & \hat{H} &= 14{,}783{\cdot}0, & \hat{G} &= 3116{\cdot}0, \\ E_{1B} &= 1699{\cdot}5, & E_{2B} &= -289{\cdot}6, & E_{1C} &= 1064{\cdot}4 \\ E_{1D} &= 1001{\cdot}9, & E_{2D} &= 608{\cdot}0, & E_{1E} &= 943{\cdot}3, \\ & & E_{1A} &= 1245{\cdot}7, & E_{2A} &= 91{\cdot}7 \\ & & E_{2C} &= -53{\cdot}3, & & \\ & & E_{2E} &= -128{\cdot}0, & & \end{aligned}$$

with a sum of squares of residuals equal to 5,854,956. The sum of squares due to fitting G, which measures the linkage effect, is the difference 10,526,166−5,854,956 = 4,671,210.

Interaction of genetic components and blocks

As defined in section 2, the genetic component g of a measurement was strictly local in application and would be expected to vary with considerable changes in the environment. A test of the existence of such variation between blocks can be made by fitting separate D's and H's to each block and testing the further reduction in the sum of squares against the remainder. We also need the separate D's and H's for obtaining the standard errors. Such a test for interaction is not orthogonal to the linkage test but, as we shall see, there is little doubt as to the existence of linkage, and so a separate D, H and G will be fitted to each block. The results are given in table 2.

TABLE 2

Estimate	Block				
	A	B	C	D	E
$\hat{D}$	10,516·9	5,915·6	9,968·7	13,852·5	8,748·1
$\hat{H}$	11,678·3	30,390·9	11,744·5	1,029·4	19,072·1
$\hat{G}$	3,112·6	3,712·8	2,967·3	2,679·1	3,108·1
$\hat{E}_1$	1,386·1	847·3	1,355·7	1,618·3	763·9
$\hat{E}_2$	4·3	249·3	−22·2	−15·1	19·3

The sum of squares of residuals is now 942,742 giving 5,854,956−942,742 = 4,912,214 as the variation of D, H, G within blocks. We therefore have the following analysis of variance

	S.S.	d.f.	M.S.	V.R.
Linkage	4,671,210	1	...	11·41
D, H, G × blocks . . .	4,912,214	12	409,351	2·171
Remainder	942,742	5	188,548	...
Pooled error	...	...	344,409	...

The interaction term is not significant and so we combine it with the remainder. Testing the linkage mean square against this combined remainder we obtain a variance ratio of 11·41, for which $0{\cdot}01 > P > 0{\cdot}001$ so that there can be little doubt of the existence of linkage. For reasons previously given the significance level should be regarded as approximate only. Reverting to the values in table 2, the mean values of D, H and G for the five blocks are $\hat{D} = 9800{\cdot}3$, $\hat{H} = 14{,}783{\cdot}0$, $\hat{G} = 3116{\cdot}0$ which are the values previously found from the fitting of a single D, H and G, as indeed they must be, since each block carries equal weight in the experiment. From the sums of squares and sums of products formed from table 2 we arrive at the following variance matrix for the estimates $\hat{D}$, $\hat{H}$, $\hat{G}$.

$$\begin{bmatrix} 1{,}658{,}011 & -6{,}180{,}692 & -205{,}398 \\ & 23{,}501{,}304 & 787{,}612 \\ & & 28{,}462 \end{bmatrix}$$

From this we obtain, *inter alia*,

$$\begin{aligned} \text{s.e. } \hat{D} &= \pm 1287{\cdot}6 \\ \text{s.e. } \hat{H} &= \pm 4847{\cdot}8 \\ \text{s.e. } \hat{G} &= \pm\ 168{\cdot}7 \\ \text{corr. } (\hat{D}, \hat{H}) &= -0{\cdot}9901 \end{aligned}$$

It will be noted that the standard errors for $\hat{D}$ and $\hat{H}$ are considerably higher than those obtained by Mather which were 808·9 and 2588·4 respectively. $\hat{H}$, however, remains significantly greater than zero.

Interaction of genetic components with years

As previously pointed out, an interaction between genotypic expression and years is to be expected on general grounds; such an interaction may not be detectable, however, if the years are too similar in their effects, or the extraneous variation swamps the year differences which do exist.

A possible result of such interaction would be that the d's and h's contributing to $W_{F2/F3}$ are different from those contributing to, say, V_{F2}. This can be tested by fitting a special constant for $W_{F2/F3}$ and finding whether the sum of squares of residuals is thereby significantly reduced. This was done for the above data and gave a reduction in the sums of squares due to fitting W as 38,618, which was not significant. It was concluded, therefore, that no detectable interaction was present.

When several years' results are available, heterogeneity of D and H is best detected by comparing the results of fitting a single D and H to all the results and separate D's and H's for the separate years. (In the latter fitting, covariances such as $W_{F2/F3}$ must have further separate constants fitted).

4. SUMMARY

1. The statistical consequences of, and assumptions underlying, a frequently-used model in biometrical genetics, are considered.

2. Differences between this model and the "classical" least-squares situation are discussed, and a new method of deriving estimates of the variance components and standard errors for these estimates is proposed.

3. A re-examination of Mather and Philip's barley data is made as an illustration of the method.

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COMPONENTS OF VARIATION UNDER SIB-MATING

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1. INTRODUCTION

MATHER (1949*a* and *b*) has described how the heritable portion of continuous variation in certain experimental populations may be partitioned into two components, D and H, the former depending upon differences in phenotype between homozygotes, and the latter upon departures in phenotype of heterozygotes from the average expression of corresponding homozygotes. Bateman and Mather (1951) considered the case of selfing after an initial cross of two inbred lines and obtained (as powers of $\frac{1}{2}$) the general formulæ for the coefficients of D and H in the different measures of variation in each generation. Nelder (1952) has described a general method of obtaining these coefficients for various systems of inbreeding and of obtaining the forms of D and H when linkage causes these to vary from generation to generation.

We have used Nelder's method to obtain the coefficients of D and H under sib-mating after an initial cross of two inbred lines. These coefficients are, of course, essential for the analysis of inbreeding experiments using sib-mating, whether as in animals as the closest possible system of inbreeding, or in plants as a system intermediate between selfing and random mating.

2. COMPONENTS OF VARIATION

Consider two alleles, A and a, of one gene, and the possible genotypes AA, aa, Aa. The possible mating pairs are given on the left of table 1, and their proportions in a population form a 6-vector which under sib-mating changes according to the transformation matrix,

$AA \times AA$	1	.	$\frac{1}{4}$	.	$\frac{1}{16}$	.
$aa \times aa$	.	1	.	$\frac{1}{4}$	$\frac{1}{16}$	.
$AA \times Aa$	.	.	$\frac{1}{2}$	.	$\frac{1}{4}$	.
$aa \times Aa$	.	.	.	$\frac{1}{2}$	$\frac{1}{4}$	.
$Aa \times Aa$	.	.	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	1
$AA \times aa$	.	.	.	.	$\frac{1}{8}$	.

Denote by S_0 the generation in which the homozygotes AA and aa are crossed, and by S_l the lth generation of subsequent sib-mating. The first two generations S_1 and S_2 coincide of course with the F_1 and F_2 of a selfing series. The proportions of mating pairs in S_l may be

obtained from the latent roots and vectors of the above matrix and are given in table 1.

TABLE 1

$AA\times AA$	$\frac{1}{5}$	$-4g(l+4)+4^{-l}$
$aa\times aa$		$-4g(l+4)+4^{-l}$
$AA\times Aa$		$g(l)-4^{-l+1}$
$aa\times Aa$		$g(l)-4^{-l+1}$
$Aa\times Aa$		$g(l-1)+4^{-l+1}$
$AA\times aa$		$\frac{1}{2}g(l-2)+2\cdot 4^{-l}$

where $g(l)=2^{-l+1}(2f(l+1)-f(l))$ and $f(l)$ is the Fibonacci series 0, 1, 1, 2, 3, 5, 8, 13, ... with $f(0)=0, f(1)=1, f(l+2)=f(l+1)+f(l)$ and $f(-l)=(-)^{l-1}f(l)$.

Following Nelder, we say that plants of generation S_k, which have a common ancestral pair in $S_l (l<k)$ but not in S_{l+1}, form an l-group. We define V_{lSk} as that item in the heritable variance of generation S_k which is given by the variance of the means of $(k-l+1)$-groups taken round the means of the $(k-l)$-groups and averaged over the latter. Hence V_{lSk} can be expressed as the difference of the total variance of $(k-l+1)$-group means and $(k-l)$-group means in S_k. We compute the variance of $(k-l)$-group means using the mean of S_{k-l} as variate while the frequencies are those of S_l.

Let d, $-d$ and h be the deviations of the phenotypes of AA, aa and Aa respectively from the mean phenotype of AA and aa. Then the contributions of the various mating pairs to the mean of S_{k-l} are given in table 2.

TABLE 2

d
$-d$
$\frac{1}{2}d+2^{-k+l-1}f(k-l+2)h$
$-\frac{1}{2}d+2^{-k+l-1}f(k-l+2)h$
$2^{-k+l}f(k-l+1)h$
$2^{-k+l+1}f(k-l)h$

Writing D for d^2 and H for h^2 we find after some reduction that

$$V_{lSk}=2^{-l-1}f(l)D+2^{-2k+1}\{4(-)^{k-l}+2^l(-)^{k-l}(3f(l-2)-f(l-1))$$
$$+2^{l-1}(27f(2k-l-2)-4f(2k-l-1)$$
$$-f(2k-2l-3)-8f(2k-2l-2)$$
$$+(-2)^{l-1}(f(2k-3l-5)+8f(2k-3l-4))\}H/25.$$

We must make one correction. Table 2 is incorrect for $k-l=1$, since in this case it gives the mean of each mating pair, while for $V_{(k-1)Sk}$ we want the variance of individuals and not of pairs about their family means. It happens, as we might therefore expect, that the above formula for V_{lSk} must be doubled when $l=k-1$. Tables 3 and 4 contain the coefficients of D and H in V_{lSk} up to $k=10$.

The formula for the coefficient of H is cumbersome, but we need only use it to calculate the nine results for $l=1, 2, 3$ and $k-l=1, 2, 3$.

Denote the coefficient of $2^{-2k+1}H$ in V_{1Sk} by $h(l, k)$. These are the figures in the main body of table 4 (but multiplied by 2 in the leading diagonal). Then

$$h(l, k+3) = 2h(l, k+2)+2h(l, k+1)-h(l, k)$$

and

$$h(l+3, k+3) = 3h(l+2, k+2)+2h(l+1, k+1)-4h(l, k).$$

These enable the remainder of the table to be constructed by extension along the rows and diagonals. As examples of the use of the tables we note that

$$V_{2S4} = \frac{1}{8}D+\frac{5}{128}H \qquad \text{(directly from tables 3 and 4)}$$

and

$$V_{4S11} = \frac{3}{32}D+\frac{6411}{2097152}H$$ (by extension from table 4 since $6411 = 2\times2450+2\times935-359$ and $2097152 = 4\times524288$).

For several genes segregating independently, D and H become Σd^2 and Σh^2. With linkage the forms of D and H change from

TABLE 3

l \ k	2	3	4	5	6	7	8	9	10	divisors
1	2	1	1	1	1	1	1	1	1	4
2		2	1	1	1	1	1	1	1	8
3			4	2	2	2	2	2	2	16
4				6	3	3	3	3	3	32
5					10	5	5	5	5	64
6						16	8	8	8	128
7							26	13	13	256
8								42	21	512
9									68	1024

TABLE 4

l \ k	2	3	4	5	6	7	8	9	10
1	2	2	3	9	22	59	153	402	1051
2		6	5	12	31	81	212	555	1453
3			22	19	42	111	287	754	1971
4				70	59	138	359	935	2450
5					230	195	450	1175	3055
6						742	627	1458	3799
7							2406	2035	4722
8								7782	6579
9									25190
divisors	8	32	128	512	2048	8192	32768	131072	524288

generation to generation, but in all cases the coefficients of D and H in V_{lSk} remain unaltered.

It should be noted that a law of conservation of heritable variation holds (Mather, 1949*b*). The grand mean of S_k is $2^{-k+1}f(k)h$. The square of the coefficient of h plus the sum of the coefficients of D and H, for given k, is always unity.

3. COVARIANCES

Let $W_{lS(k-1)k}$ be the covariance between $(k-l)$-group means in S_k and S_{k-1}. Instead of using the squares of terms in table 2 with the frequencies of table 1 we construct an auxiliary table from table 2 by replacing k by $k-1$ and then use the products of corresponding terms from table 2 and the auxiliary table with the frequencies of table 1. Hence

$$\begin{aligned} W_{lS(k-1)k} = 2^{-l-1}f(l)D + 2^{-2k+2}\{&2(-)^{k-l-1} \\ &+2^{l-1}(-)^{k-l}(f(l-1)-3f(l-2)) \\ &+2^{l-1}(27f(k-l-3)-4f(2k-l-2)) \\ &-f(2k-2l-4)-8f(2k-2l-3) \\ &+(-2)^{l-1}(f(2k-3l-6)+8f(2k-3l-5))\}H/25. \end{aligned}$$

The coefficients of D are independent of k and are the same as for V_{lSk}. Table 5 contains the coefficients of H. Once the first nine terms have been evaluated the table may be extended using the same relations as for the variance table. Since $k-l>1$ a correction like that in the previous section is not needed.

Examples $W_{1S23} = \frac{1}{4}D$ (Tables 3 and 5.)

$$W_{4S67} = \frac{3}{32}D + \frac{81}{4096}H \qquad \text{(Tables 3 and 5.)}$$

Covariances between means m generations apart may be denoted by $W_{lS(k-m)k}$. The coefficients of D are the same as before, and

TABLE 5

l \ k	3	4	5	6	7	8	9	10
1	0	2	5	14	36	95	248	650
2		2	7	19	50	131	343	898
3			6	25	67	178	465	1219
4				22	81	219	578	1513
5					70	265	715	1890
6						230	857	2315
7							742	2777
8								2406
divisors	16	64	256	1024	4096	16384	65536	262144

the coefficients of H may be obtained simply from tables 4 and 5 as follows. Let $h(l, k, m)$ be the coefficient of $2^{-2k+m+1}H$ in $W_{lS(k-m)k}$. Then $h(l, k, m+2) = -h(l, k, m+1)+h(l, k, m)$. This means for example that the main body of the $W_{lS(k-2)k}$ table is the difference of the main bodies of tables 4 and 5, and the divisors in the $W_{lS(k-2)k}$ table are half those in table 5.

Examples $V_{3S7} = \frac{2}{16}D+\frac{111}{8192}H$ (Tables 3 and 4.)

$W_{3S67} = \frac{2}{16}D+\frac{67}{4096}H$ (Tables 3 and 5.)

$W_{3S57} = \frac{2}{16}D+\frac{44}{2048}H$ (since $44 = 111-67$).

$W_{3S47} = \frac{2}{16}D+\frac{23}{1024}H$ (since $23 = 67-44$).

4. SUMMARY

The coefficients of D and H in the different measures of continuous variation are obtained for the generations of a population started by a cross between true breeding lines and maintained by continued sib-mating. The coefficients are set out for generations up to S_{10} in tables, 3, 4 and 5.

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PROGRESSIVE IMPROVEMENT IN SELF-FERTILISED CROPS

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WHEN breeding for increases in quantitative characters by hybridisation, the objective is usually to produce varieties surpassing any available as parents. Akerman and MacKey (1948) aptly call this transgressive breeding. With this sort of breeding any parental combination may be useful, but with crops which have been cultivated and selected over a long period, most are of no value. For instance, at the New Zealand Wheat Research Institute, where increase in yield is one of the main objectives, of some 300 crosses which have been grown sufficiently long for their worth to be estimated, only three have produced new varieties, one of them producing two, while only 24 have produced lines of merit sufficient to warrant test in extensive field trials. Good crosses are obviously rare, and should therefore be utilised to the fullest extent possible.

All the evidence indicates that a large number of genes determines the expression of most quantitative characters, and that a large number of genes determining these characters is segregating in most crosses. Where a large number of genes is segregating, the frequency of any one genotype in the segregating population is low. The homozygous genotype with the maximum character expression will be present with the frequency of $1/4^n$ in F_2 and $1/2^n$ when segregation is complete. (n = the number of segregating gene pairs). Where many genes are segregating, the chances of producing or finding this genotype are remote. But this, the "ideal", will not be the only useful genotype in the hybrid population. If both parents of the cross contribute a substantial number of segregating plus genes to the cross, there will be numerous homozygous genotypes in the population with a higher character expression than either parent. Assuming, for instance, that each parent contributes ten independently segregating plus genes, individuals homozygous for more than (say) 15 plus genes would be valuable.

The relative frequencies of homozygous individuals with more than 15 unlinked plus genes when segregation is complete are set out below.

Number of plus genes	16	17	18	19	20
Frequency (all over 2^{20})	4845	1140	190	20	1

These frequencies show that valuable genotypes will occur in reasonable numbers in moderately large populations. They also

suggest that the successful selections from any hybrid population probably do not represent the genotypes with the highest expression which can possibly occur in that population. Crosses which have yielded valuable lines are therefore promising sources for breeding or selecting still further improved lines.

This may be done in two ways. The first is to grow large F_2 populations of the desired crosses and select from them, or from later generation populations derived from them. The likelihood of producing lines with the highest possible expression by this method is remote. For instance, lines with yield equal to that of F_1 are still an objective, not an achievement, in most plant breeding schemes (Ellerton, 1944).

The second, suggested here, is based on the following considerations. If several high-yielding lines are isolated from a cross it is unlikely that they will all contain the same plus genes. Those missing from one line will probably be present in another. In the hypothetical case quoted above, there are $4845/2^{20}$ homozygous lines with 16 plus genes. If any two such lines are crossed, in 1820/4845 of the cases each parent will contain four different plus genes; in 2240/4845 of the cases they will have one gene pair in common and hence will contain three different plus genes; in 720/4845 cases they will both lack two particular plus genes; in 64/4845 cases they will both lack three particular plus genes, and in 1/9690 cases they will be identical. The probable results of such a crossing scheme are tabulated below, each cross being carried without selection until segregation is complete.

Number of genes by which parents differ	Probability of their being crossed	Number of homozygous genotypes according to numbers of plus genes					Total population
		16	17	18	19	20	
8	1820/4845	70	56	28	8	1	256
6	2240/4845	20	15	6	1		64
4	720/4845	6	4	1			16
2	64/4845	2	1				4
0	1/9690	1					1

The chances are heavily weighted in favour of producing populations with relatively high frequencies of the highest, or near highest, yielding genotypes. They will be much more common than in the original F_2 or unselected populations derived from it, so that smaller segregating populations can be used with greater prospects of success.

This, then, appears to be a much surer and more economical method of utilising the potential advantages of a successful cross than selection from the original hybrid population. Two or three cycles of such selection and crossing should assemble the major linkage groups determining maximum expression of a character in

one or a few homozygous lines. Comparison of character expression in such a line with that in F_1 will show whether or not further cycles to disrupt these linkage groups would be warranted.

The most obvious disadvantage of the method is that it is slow. Each cycle could hardly take less than six years ; it would probably take ten. It is not suggested that all the facilities of a breeding institution be devoted to this intensive treatment of a few crosses. As the amount of ultimate progress is restricted by the genic constitution of the original parents of the cross, such a course would be unwise ; as good results can be expected with relatively small populations, it is unnecessary. Rather, one would suggest that when they are found outstanding parental combinations be treated in this manner, while the search for such crosses continues.

SUMMARY

In transgressive breeding for quantitative characters valuable crosses are rare. Therefore, when found, they should be utilised fully. If many genes are segregating in any particular cross the ideal combination occurs but rarely, but other combinations short of perfection will be useful and relatively common. Lines selected from crosses therefore probably belong in this latter category. Crossing together high yielding lines isolated from the same cross will give populations with a relatively high frequency of the higher yielding genotypes, and will be the surest and most economical method of producing the highest yielding genotype. Such a programme would be a useful adjunct to normal breeding programmes.

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THE BLOOD GROUPS OF THE SHONA OF SOUTHERN RHODESIA

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THIS paper describes the results of tests for the ABO, MN and Rh blood group systems, carried out on specimens collected in Salisbury, Southern Rhodesia, from members of the Shona tribes. The majority of the persons tested belonged to the Northern Shona group. Tests were carried out locally for the ABO groups of 377 persons, and a further 101 specimens were sent to London where ABO, MN and Rh groups were determined. Gene frequency calculations were done by the methods described by Chalmers, Ikin and Mourant (1949), and Prasad, Ikin and Mourant (1949), and more fully described by Mourant (1953).

The only previous anthropological blood grouping work done in this region is that of Elsdon Dew (1939).

The A and B gene frequencies calculated from the present work, 15·7 per cent. of A and 13·4 per cent. of B, fall just within the range of rather scattered frequencies found for the Northern Shona tribes by Elsdon Dew. Our values for both genes are near the upper end of Elsdon Dew's range and are near to the values found by him for the Korekore tribe of the Northern Shona group. Members of this tribe probably form a considerable proportion of our subjects but not a majority of them. Elsdon Dew's gene percentages for the Northern Shona as a whole are only 14·6 per cent. of A and 11·2 per cent. of B. For our MN frequencies there is no previous work anywhere in East and South-East Africa with which we can make comparisons. The results agree well with numerous recent unpublished observations in various other parts of Africa.

The Rh frequencies have a typical African aspect. As far as published papers and work now in progress can show, the differences between different parts of Africa in this respect are slight and only in a few cases statistically significant. The *cDe* chromosome is everywhere the commonest by a very wide margin, but is most frequent in the centre and east. In the west and south, however, *cde* shows higher frequencies than in the east and centre. The E gene also tends to have a higher frequency in the centre. In these respects the Shona appear, as far as the small number tested can show, to agree with the peoples of West and South Africa rather than with those of the centre.

They also differ, though barely significantly, from those of East Africa (Kenya and Uganda), (Allison, Ikin and Mourant, 1952 ;

TABLE 1

ABO groups of the Shona

Group	Number observed	Frequency observed	Frequency expected	Number expected	Gene frequencies
O . . .	235	0·492	*0·502*	*240·1*	**0·709**
A . . .	124	0·259	*0·248*	*118·4*	**0·157**
B . . .	105	0·220	*0·208*	*99·3*	**0·134**
AB . .	14	0·029	*0·042*	*20·1*	...
Total . .	478	1·000	1·000	477·9	1·000

TABLE 2

MN blood groups of the Shona

Group	Number observed	Frequency observed	Frequency expected	Number expected	Gene frequencies
M . . .	27	0·267	*0·275*	*27·8*	**0·525**
MN . .	52	0·515	*0·499*	*50·4*	...
N . . .	22	0·218	*0·226*	*22·8*	**0·475**
Total . .	101	1·000	1·000	101·0	1·000

TABLE 3

Rh blood groups of the Shona

Phenotype	Principal genotype	Number observed	Frequency observed	Frequency expected	Number expected
ccDee . .	R_0R_0	71	0·703	*0·674*	*68·1*
CcDee . .	R_1R_0	8	0·079	*0·120*	*12·1*
ccDEe . .	R_2R_0	9	0·089	*0·111*	*11·3*
CCDee . .	R_1R_1	1	0·010	*0·005*	*0·5*
CcDEe . .	R_1R_2	4	0·040	*0·009*	*0·9*
ccDEE . .	R_2R_2	0	0·000	*0·004*	*0·4*
ccD^{u}ee . .	R^u_0r	2	0·020	*0·019*	*1·9*
ccddee . .	rr	6	0·059	*0·057*	*5·8*
	Total .	101	1·000	0·999	101·0

Chromosome frequencies

cDe	R_0	0·591
CDe	R_1	0·069
cDE	R_2	0·064
cD^{u}e	R^u_0	0·037
cde	r	0·239
		1·000

Ikin, Mourant and Raper, 1952), but the Shona are nearer in their Rh frequencies to the Bantu-speaking Kikuyu than to the Nilotic

Luo. It is, however, desirable that the blood groups, and especially the Rh groups, of the inhabitants of the intervening area should be examined.

There is some evidence that one important basic component of many African populations has an Rh composition near to that of the Shona, a second with higher frequencies of cDe and cDE, but lower cde, being typified by the Pygmies of the Belgian Congo (Hubinont and Snoeck, 1949). A detailed account of the variations in frequency of the Rh groups among Africans and of their possible significance is given by Mourant (1953).

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COMMENT AND REVIEWS

MICROBIAL GENETICS, Papers in Bacteria and Bacterial Viruses selected by Joshua Lederberg. University of Wisconsin Press : Madison. 1951. Pp. 303. $3.75.

The re-issuing of articles, selected from several scientific journals, on bacterial genetics, comes at a fit time, for despite the publication of Burnet's pioneer work on resistance to phage in 1929, it is only ten years since geneticists realised the possibilities of micro-organisms as a fruitful field for research. Professor Lederberg's prime purpose, however, in producing this volume on Microbial Genetics was to make the original literature accessible to the student. This he has done with the nicety of discrimination that was required with only 300 pages at his disposal. There are twenty original papers from genetical, bacteriological and biochemical journals, an introduction and a bibliography. An adequate introduction for any student. But this volume has another use. The research worker, whether he has specialised in micro-organisms or not, will find it a great help in bringing the recent work on bacterial genetics into the general picture of genetics and biology.

From the genetical viewpoint the short life cycle and the astronomical numbers that can be cultured make bacteria well suited for mutation studies ; and in fact mutation was for many years the only way of studying bacterial genetics. However, there are many difficulties of interpretation in mutational work in bacteria, and some of these are evident from the papers by Luria and Delbruck, Lea and Coulson, Newcomb and Demerec. Furthermore, bacteria are good material for elegant screening methods which are essential for mutational studies ; this is well brought out in the paper by Davis on " Nutritionally deficient mutants isolated by means of penicillin."

The main outcome of the mutation work has been to show that many examples known to bacteriologists as " training " or " adaptation " are due to the selection of rare mutants, pre-existing in the colony, which can grow on the strange medium used for the test. The other important result is that mutation rates may be as low as 10^{-10} per bacterial fission.

Mutations in bacteria are induced by the same agencies as in higher organisms. The rate of mutation, as in higher organisms, varies with the organism and the gene studied. All these results are extensions to the lower organisms of principles known from plants and animals. They demonstrate the universality of the genetic system. But the finding by Demerec of such low mutation rates as 10^{-10} for resistance to drugs in *Escherichia coli* is something well beyond the order which has been practicable to measure in higher organisms. It is significant too that this example of an extremely low mutation rate causes a change which could be construed as a new and constructive effect—the ability to thrive in an extreme environment in which the organism has never before been placed. If other new and constructive changes, which have hitherto not been found, are of this order of rarity in higher organisms then this low mutation rate is of considerable importance in formulating concepts of selection and evolutionary rates.

As the bacterial cell is, in a sense, equivalent to the germ cell in higher

organisms the generative nucleus of bacteria is in much closer contact with its environment than in higher organisms which are protected by somatic tissue. It might be expected, therefore, that bacteria might be the best organisms for showing directed change in the genotype by alteration of the environment. The transforming nucleic acids which change the antigenicity of *Pneumococcus* described in the well-known paper by Avery *et al.* would appear to be an example of such a change. But the superficial nature of these antigens throws some doubt on their relevance to nuclear heredity; it may be another example of the alteration of the cytoplasm and not of the nucleus. May we not have here a distinction which exists in higher organisms between cytoplasm and nucleus—a distinction which has only become understood in the last ten years?

This directed change reminds one of the possibility of directed adaptation which is still accepted by the Hinshelwood biochemical school to be a common phenomenon in bacteria. It is unfortunate that the opportunity afforded by this volume to clarify the misunderstandings between the two schools of thought was not seized. Instead of the brief statement that " it is essential to keep in mind physiological adaptations which are non-heritable, but whose interplay with heritable changes may trap the unwary ", a full account with a selected article from the biochemical school might have had a salutary effect.

To most geneticists who have worked with higher organisms the facts obtained from experiments which show changes in a micro-organism due, in some cases, to the selection of gene mutations and in other cases to adaptation without mutation are exactly what he would have expected; and there are enough cases of both to show that both do exist. In this respect a useful analogy to a plant geneticist is to consider a bacterial colony as a differentiating organism. Then adaptation which is not due to selection of mutants can be visualised as equivalent to differentiation in a higher organism. Just as the higher organism changes the environment of its somatic cells during differentiation, so a bacterial colony changes the environment of its component cells by depletion of substrates or by the accumulation of staling products. Also, just as the higher organism utilises different genes—all of which are present in every nucleus—at different stages in its differentiation so does a bacterial colony in its process of adaptation. What the biochemical school have called alternative reaction networks, the geneticist might describe as alternative gene systems. Examples of alternative gene systems in plants can be found, for example colour inheritance of plants in which independent genes produce the same pigments in the different cellular environments that are present in different parts of the plant.

Adaptation in micro-organisms from the genetical standpoint simply means that the facility to adapt is genetically determined. That this genetically determined capacity for adaptation in bacteria is not uncommon is not surprising in view of the ever-changing environment surrounding these bacterial cells. The main difference between the bacteria and higher organisms is that these adaptations may be carried over from one sexual generation to another in bacteria, whereas in higher organisms this is rare. When more is known about the relative frequencies of sexual and mitotic divisions in bacteria it may be that this difference will disappear.

There are two points to consider in this respect. Higher organisms,

because of their complex differentiation of the soma, must start their differentiation in the zygote from a genotype which varies only within rather narrow limits; this includes the nucleus and cytoplasm. For the environment of the zygote is constant and often rigorously controlled and unless the genotype is nearly constant and unaffected by the changes of differentiation in the preceding generation then the organism begins life and differentiation not at the beginning but at the end. Such an isolated genotype which is essential to the well-being of higher organisms might well be a disadvantage to bacterial cells which, right from the beginning of their lives, are in danger of a big change in their environment.

The other point is that despite the advance made in bacterial cytology it is not known whether there are any special cells which are the result of a sexual process and which are isolated cytoplasmically. Clearly they are a possibility but bacteria could well get on without them.

One great drawback at the beginning of bacterial genetics was the lack of knowledge of the genetic system. Now, since the elegant experiments of Lederberg which have demonstrated linkage and crossing-over, a more exact genetical analysis is possible. In surveying bacterial genetics it is clear that genetics has contributed greatly to bacteriology. And it is perhaps reasonable that our knowledge of the gene in the last decade has not come from bacteria but from *Drosophila*, higher plants and fungi. It is to be expected that in the next ten years, now that the bacterial genetical tools have been made that bacteria will reciprocate by contributing to genetics.

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BLOOD GROUPS IN MAN. By R. R. Race and Ruth Sanger. Oxford: Blackwell Scientific Publications. 1950. Pp. 290. 30s.

In their preface to this book the authors tell us that another volume in the series (by Dr A. E. Mourant) will deal with the human blood-groups and ethnology, and a third (by Dr P. L. Mollison) with the clinical aspects. This is a wise sub-division. Apart from the special application to ethnology, the present volume provides just what is wanted by the student of genetics, for it describes most lucidly and with all necessary detail the inheritance of the various blood-groups, giving at the same time sufficient, but not too much, information on the serological background.

The history of the growth of this particular subject must be one of the most remarkable in genetics. The original ABO system was discovered in 1900 and until 1927 remained the only one known. In that year the existence of two more was established. That was the state of knowledge in 1934 when Professor Fisher, perceiving with characteristic foresight that this was one of the best, if not the best, subjects for research in human genetics, founded a unit at the Galton Laboratory under the late Dr G. L. Taylor, who was soon joined by Dr Race. So it was that a British school was ready to play a very large part in the developments that came so rapidly from 1940 onwards. During the last twelve years no fewer than six additional blood-group systems have been discovered, the latest of them after this book was written. So there are already markers for nine of the twenty-three autosomes, or ten if the ability to taste phenyl-thio-carbamide (which has been described as a sort of honorary blood-group) is added to the list. As with other forms, so it will probably happen in

man, that once linkages commence to be picked up, they will be detected at an ever-growing pace.

The first impression likely to be made on students of genetics is the utter simplicity, speaking genetically and not serologically, of the human blood-groups. Those who established the present structure of formal genetics have been accused of using only the good genes, those that mendelise neatly, and ignoring the bad ones, whose effect is obscured by genetic and environmental interactions. In this field there are no bad genes. There are no environmental interactions. Each gene corresponds to an antigen on the surface of the erythrocytes. Furthermore, dominance is usually, perhaps always, absent. Each of the allelomorphic genes in each system determines an antigen for which, sooner or later, an antiserum is forthcoming by which its presence can be detected. Thus the Duffy group, of 1950, was discovered by means of an antiserum which reacted with the Duffy positive cells possessed by those who have one or two doses of the corresponding gene. But an anti-serum that would react with heterozygous and Duffy negative blood was confidently anticipated, and it has duly appeared. So it has been with the Kell system and the S,s component of the MN system ; and so it may be in due course with all the others. For these reasons the working out of the genetics of each system has followed almost immediately on the heels of the serology, the actual amount of family investigation needed being almost absurdly small in comparison with what is required in many other fields.

The blood-groups have much to contribute to genetics in addition to their practical use in connexion with blood-transfusion, or in the study of hæmolytic disease, or in ethnology, or as chromosome markers. The complexities, if that is not too strong a word, are likely to make an increasing contribution to genetic theory. When Fisher propounded his theory of three closely linked loci to account for the intricacies of the Rhesus system, the most immediate reaction was probably the gasp of relief from those who teach students. Then came almost immediate verification of the predictions made by the theory and there is other supporting evidence as well. Fisher pointed out that given the frequencies of the three common Rhesus combinations in Western Europe, the frequencies of the rarer combinations could be accounted for by crossing-over ; and it now appears that this may be true of other populations with different common combinations. He was led by this argument to suggest that the order of the loci on the chromosome was DCE, a supposition that was brilliantly confirmed by the discovery of a deletion involving the C and E loci, the story of which forms a worthy postscript to Race and Sanger's book. Now it would appear that the M, N and S,s components of the MNSs system also depend on a pair of closely linked loci, and perhaps other groups may behave in the same way. Clearly the conception of closely linked genes with allied effects is one to be taken very seriously and this is an excellent field in which to study it. There are a number of other points also at which blood-group genetics may well contribute to the whole subject, for example, the possible step allelomorphs of some of the rarer Rhesus genes and the indications of competition for a common substrate.

Race and Sanger have written an excellent chapter on problems of parentage and identity. They show that an expert laboratory equipped with the necessary antisera could exclude about 62 per cent. of wrongful

accusations of paternity. It is most unfortunate that so little use is being made of this knowledge. The creaking legal machinery needs complete reconstruction and it is to be hoped that one of the results of the publication of this book and of all the work that lies behind it may be the revival of Lord Methyr's bill, which lapsed owing to the outbreak of war in 1939.

Workers in many fields have reason to be grateful to Race and Sanger for writing this book, and of these not least the geneticists. It is so much a model of what such a book should be that one feels ill-disposed to offer any criticisms (except perhaps to say that the bibliographies would be more convenient if they were arranged alphabetically). Such criticisms could only be trivial. This is a first edition and a new one is sure to be demanded very soon ; the authors can be trusted to make better improvements in matters of detail than any that could be suggested by well-meaning critics.

J. A. Fraser Roberts.

THE NEW YOU AND HEREDITY. By Amram Scheinfeld. London : Chatto and Windus. 1952. Pp. 618+xv. 25s.

You and Heredity requires little introduction. First published in 1939, it achieved a very large circulation in the U.S.A., and besides a separate publication in Great Britain it was translated into several other languages. The new edition has been almost entirely rewritten and has expanded in the process until it is half as large again as its predecessor. For this the author gives two reasons, the growth of human genetics in the past decade and his own increasing knowledge and understanding of the subject. Certainly the coverage is comprehensive enough : there are very few features of man which are not discussed.

The author, very properly, does not set out to give a textbook of genetics. Rather he aims at providing a sufficiency of the basic principles to make possible a discussion of man, in all his aspects, as a product of the joint action of heredity and environment. He covers physical and functional features, disease, deformity, twins, mental capacity, sexual upsets, blood groups, longevity, social behaviour, personality and crime, winding up with chapters on evolution, race, eugenics, population problems, and the future. The treatment is full, with frequent reference to the work and views of specialists, chiefly American, in the various fields. Many of the topics, mental capacity and crime for example, are of course sources of dispute rather than agreement. The author does not shirk these issues ; on the contrary he does his best to present the case from all points of view. This must obviously lead to a certain diffuseness in the discussion ; but the sooner the lay-reader, for whom the book is intended, realises that in much of human genetics final answers are the exception rather than the rule, the sooner he will appreciate how urgent it is to push on with research. If by his presentation of the problems Mr Scheinfeld helps to dispel some long cherished illusions and arouses a wide interest in achieving true solutions, he will more than repay genetics for the material it has provided him.

On the technical side some criticisms must be made. The book contains certain false statements such as that " . . . genes are highly complex protein molecules, composed chiefly of nucleic acid, which is the basic material of all protoplasm . . . " (p. 57). Some old and popular loosenesses of usage are perpetuated, as when it is said that " . . . Darwin held . . .

that in this struggle for existence, the fittest would survive ", so leaving open the question of " Fittest for what ? " (p. 481). The survival of the fittest was Spencer's phrase, not Darwin's, and no one reading Darwin could believe that he related natural selection to the mere survival of individuals, or could have any doubts as to what constituted fitness. Nor is the presentation of the technical genetics always clear : it is not, for example, easy to understand the formal inheritance of eye-colour differences from Chapter II, nor can any real understanding of meiosis be gleaned from the figure on p. 14. The style too is irritating at times. " We know at last what a human sperm carries—the precious load that it fights so desperately to deliver . . . " (p. 6), and " . . . the plump Abbot Gregor Mendel, waddling about in the garden . . . resolved to confine his studies to his own little patch and not to wander afield (possibly because he was too fat to travel comfortably) . . . " (p. 52). To say the least, this is an ungracious description of a great scientist, unnecessary even if historically true, which, so far as I am aware, it is not. " Biologists " we are told in the brief historical survey of genetics " were floundering about in confusion " before Morgan (p. 55), while no reference is here made to such men as Johannsen, who was responsible for the clear statement of the relation of phenotype to genotype and environment which provides the theme of the book, and Bateson, who did more than anyone else to establish that " the mechanism of heredity is almost the same in all living things ", a principle that Mr Scheinfeld (p. 3) properly describes as one of the amazing, and we might add basic, discoveries of genetics. Surely, if such is his wish, he could do honour to his fellow countryman without failing to give credit to such other great figures of the past.

These comments, however, should be taken more as warnings for the student than discouragements for the general reader. The book should be judged by the standards of its aims. It is not a textbook, even though some may seek to use it as such ; but it is very much more than the tittle-tattle which so often passes for popular science. It is a valuable attempt to set before the layman an honest picture of himself as the product of his hereditary endowment and his environmental circumstances. The picture is necessarily neither complete nor always clear—if such were possible human genetics would be at an end—but it provides much information, dispels many myths and sets some of the great social problems of our time in a new and truer light. It could be read with profit by all who seek a better understanding of themselves and the society they live in. Wide appreciation of the knowledge, considerations, problems and issues set out in *You and Heredity* is essential if our society is to prosper. It is not enough that we geneticists should discover these things, formulate these problems and come to these conclusions : they and their implications are basic to our well being and must not remain hidden in learned journals and specialist texts. In setting them out for a wider audience Mr Scheinfeld does a service to us all.

K. MATHER.

AN INTRODUCTION TO THE EMBRYOLOGY OF ANGIOSPERMS. By P. Maheshwari. New York, Toronto, London : McGraw-Hill Book Company, Inc. 1950. Pp. 453+x 55s. 6d.

Embryology is concerned with the development of the spores, the germ cells, the embryo and the endosperm in the higher plants. Its description

has been given a tentative coherence by the theory of evolution with its subordinate inferences of homology and phylogeny. Professor Maheshwari's book, after an excellent historical introduction, follows this classical pattern with care and success. The homology and the phylogeny may be dubious at the cellular level but they are relegated with experimental questions to the end of the book and therefore cast no shadow over the descriptive body of the book.

There is however a fundamental means of unifying embryology and of thus giving it scientific uses and applications. Students of genetics and physiology will see these uses on all sides. They will notice that the developments described lead to and from meiosis and fertilisation. These two processes are the central facts of the plant's life determining profound changes in the properties—physiological and genetic properties—of the cells taking part.

These effects are not noticed by Maheshwari. Nor indeed does he notice how the different types of plant development are bound up with new experimental fields of enquiry. Different forms of pollen development illustrate principles of cell-differentiation, cell physiology and properties of hereditary variation and natural selection. The same is true of the endosperm and the embryo with their variations in sexual and subsexual reproduction. The experiments of Renner on embryo-sac competition in *Œnothera* are no less fundamental to embryology than they are to genetics, physiology and biochemistry. The unicellular stage of development in the higher plants is indeed a focus of scientific enquiry. And the last person to realise this is, apparently, the embryologist !

In all these directions a genetic vacuum is apparent in Maheshwari's book. It is a vacuum which has persisted because embryology is a laborious study in the enquiry and perhaps even more in the reading of it. Embryology is however capable of taking us forward as much as the genetics of micro-organisms—another long-neglected study—is already doing. To provide the basis of this advance it will however be necessary for the author of a work on embryology to extend his interests to papers which introduce other ideas than those of the last century. C. D. DARLINGTON.

THE GENETICS OF THE DOG. By Marca Burns, B.Sc. Edinburgh : Commonwealth Bureau of Animal Breeding and Genetics. 1952. Pp. vi+121. 12s. 6d.

Dog breeding is full of pitfalls and dog breeders are full of folklore. Miss Marca Burns endeavours to introduce some genetics to them. She covers a wide field but her understanding of it is not entirely clear. Half-way through her book, she discovers, almost to her own surprise, that " The orthodox theory that inheritance is entirely determined, at the time of fertilisation, by the genes which the fertilised egg happens to contain, is in some respects illogical." In these circumstances she feels compelled to admit that " Lysenko's explanation of a direct effect of the environment on the heredity (after a few generations) is attractive." Lysenko is right. Or, at least, that he would have been right if he had ventured to talk about animals.

It is not remarkable that Miss Burns should hold these views. The same views were held in the same place, Edinburgh, by Professor James Cossar Ewart before Miss Burns or, for that matter, Lysenko was born.

In any case these views are still held by illiterate people all over the world. What is remarkable is that they should now be expounded in this country coupled with the name of Lysenko. And that they should be expounded under the auspices of an agency supported by national funds and intended for the publication of useful information : the Commonwealth Agricultural Bureaux. C. D. DARLINGTON.

SYMPOSIUM ON RADIATION MICROBIOLOGY AND BIOCHEMISTRY. Sponsored by The Biology Division, Oak Ridge National Laboratory. Reprinted from *J. Cell Comp. Physiol.* Vol. 39, Suppl. 1. 1952. Pp. 128.

There are seven papers and three abstracts in this Symposium.

W. M. Dale is concerned with the evidence that X-radiation acts in causing mutations through intermediate products especially OH radicals and H atoms. Using the principle that one solution should accordingly " protect " another from X-ray damage, Dale has carried out experiments which suggest either a chain reaction or an activated state in the protector molecule.

L. H. Gray discusses the physical and biological evidence of the nature of the energy transfer from ionising particles. He points out the possible difference in regard to dispersal of damage between chromosome fragmentation and inactivation of viruses or spores. Zirkle and others attempt to show with survival curves that the latter effect is very rapid.

Hollaender and others show the effects of water content and oxygen pressure on mutation in *Aspergillus* spores. Swanson suggests that ultraviolet mutation rate is increased by nitrogen mustard pre-treatment. Newcombe proposes that bacteria should be regarded as haploid and therefore genetically irreducible. This is more of an assumption than it may seem. C. D. DARLINGTON.

BOOKS RECEIVED

PROCEEDINGS OF THE SOCIETY FOR THE STUDY OF FERTILITY. No. III Cambridge Conference. Cambridge : Heffer. 1951. Pp. 79. 10s.

A useful discussion by 13 British and American workers of the causes of sterility chiefly human from all aspects except the genetic. A Danish visitor however gives the evidence that absence of the vas deferens is hereditary in cattle.

PFLANZENZÜCHTUNG. 1. GRUNDZUGE DER PFLANZENZÜCHTUNG. By Hermann Kuckuck. Berlin : Walter de Gruyter & Co. 1952. Pp. 132, illus. 10½ × 15½ cm. Paper covers.

GENERAL GENETICS. By Adrian M. Srb and Ray D. Owen. California : W. H. Freeman & Co. 1952. $5.50 (47s.).

FIFTH CONFERENCE ON PLANT BREEDING

ABSTRACTS of Papers read at the FIFTH CONFERENCE ON PLANT BREEDING held at BAYFORDBURY on 24th-26th JULY 1952 under the auspices of the AGRICULTURAL RESEARCH COUNCIL

AIMS AND METHODS IN PLANT BREEDING

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Aims in plant breeding depend upon several factors—the type of crop, the climate and soil in which it is grown, prevalence of disease, etc.—but one obvious factor in deciding what characters to concentrate upon is the past breeding history of the species.

Handsome returns to the breeders' work will be obtained with most characters in (1) natural species which have not been cultivated and therefore have not been selected either consciously by the breeder or unconsciously by the ancient husbandman. (2) Well-bred and cultivated species in an environment outside the range of their past cultivation. (3) In cultivated species which have been maintained as vegetatively reproduced clones in which seed production is rare. These three classes of species can be improved by breeding without much regard to careful discrimination of objectives. They require no further consideration here.

With highly bred species the situation is very different. A profitable return will only come from concentrating on *virgin* characters, *i.e.* characters which have not received attention in the past. Such characters are likely to be those which have been beyond the means of the unorganised breeding and unconscious selection of the past centuries—disease resistance, processing qualities, and phenotypic stability, *i.e.* the ability to reach a norm of phenotypic expression in a wide range of environments.

Breeding for disease resistance, processing qualities, etc. often require new techniques, and the success of such work largely depends upon rapid and efficient methods of assay. For example testing disease resistance on small seedlings and the analysis of sugar beet for sugar and noxious nitrogen on small amounts of material.

The ability to attain a phenotypic norm under widely different conditions, is a character the testing of which may require several different localities. Controlled environment chambers are a great help for detailed analysis of the genetic and physiological factors involved and also for a reproducable testing sieve for the plants.

I have been studying the interaction between genotype and environment for the last four years using the tomato as the test plant and the number of flowers in the inflorescence as the character. Temperature during the first 20 days of seedling growth was the environment studied. Preliminary experiments in 1949 and 1950 and the final experiment in 1952 all show that different parental pure lines show different degrees of phenotypic stability. The F_1 hybrid is much more stable than either of the parents and the stability in the F_3 generations ranges from that of the highly stable F_1 to that of the least stable parent. This clearly demonstrates that phenotypic stability is under genetic control and therefore will respond to selection.

A similar greater stability of the F_1 hybrid was described in *Potentilla glandulosa* under mountain and coastal climates by Clausen at the International Genetics Congress in 1948. Mather (1950) found in *Primula sinensis* that the F_1 was less variable not only *between* plants but also *within* plants than the pure line parents. Haskell (1952), comparing pure lines and F_1 hybrids in maize for four characters found that hybrids varied less than pure lines under unsuitable environments.

How general is this stability of F_1 hybrids only future work will tell, but if it is general then the economics of F_1 hybrid seed production in a number of cultivated plants should be reconsidered. For, the optimal size in many crop plants is already below the maximum attainable, and the hybrid vigour of F_1's would be of little advantage. But greater stability and reliability of performance in different localities and in different years is a factor of prime importance and warrants an all-out drive to breed F_1 hybrid seed, which can be produced cheaply. To do this emasculation of the mother parent must be genetic and not manual. Male sterility has been used in onions and tomatoes. Since male sterility is usually controlled by a recessive gene and is a defective character it is highly probable that X-rays would be effective in producing it in species where it is not already at hand.

Genetic emasculation can also be devised on a basis of self-incompatibility but it is necessary to know whether the *Nicotiana-Œnothera* or the *Crepis-Parthenium* systems are at work. The choice of emasculation method, whether it is male sterility —genic or cytoplasmic—or incompatibility will depend upon such factors as the ease of vegetative propagation and whether the reproductive or vegetative part of the plant is the commercial product. With all the available methods it seems possible to produce cheap hybrid seed in most crops except those which are irretrievably cleistogamous. The great advance in maize production by the use of F_1 hybrids in the U.S.A. should serve as a confident background to a much wider application of the method.

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REPRODUCTION OF IMPROVED STOCKS

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The breeding and scientific assessment of improved types in relation to agro-ecological conditions can only lead to increases in food production in so far as the seed stocks offered to the grower reproduce the essential characteristics of the type. (Gregor and Horne, 1935). Strenuous efforts have been made by many commercial seedsmen and specialists but results of surveys of seed stocks often prove disappointing (North and Squibbs).

1. Confusion of identity is frequent in populations such as Wild White Clover and named types of brussels sprout which are distinguished mainly by quantitative characters. It appears to be more frequent in types known by numbers easily confused with other numbers such as S.23, Diamond II, Hybrid 29, Squareheads II. Some particularly valuable stocks, while they are in short supply, have shown a higher proportion of confused stocks and this is a class in which a high measure of authenticity is most desirable (Hawkins, 1951).

2. Synonyms constituted 75 per cent. of the names given to potato varieties until these were identified and classified by the National Institute of Agricultural Botany (N.I.A.B.). Recent work by North has shown that 70 per cent. of french bean varieties are synonyms. Under such conditions the grower may buy a variety as a novelty which is already known, under an older name, to be unsuited to his conditions.

3. The opposite position is also found among commercial seed stocks in that the same name may be given, as in Eldorado french bean and some strains of sugar beet, to two different and unrelated stocks.

4. Deterioration of stocks through genetic variation occurs most rapidly in types which are normally cross-fertilised. In surveys of Cambridge No. 1 brussels sprout

60 per cent. of commercial seed stocks differed from the certified stock in varietal purity by more than 10 per cent., while of 66 stocks 9 were no longer recognisable as containing plants of the named type (*cf.* H.M. Stationery Office : Report on Seeds).

Through the co-operation of progressive seed growers, with the plant breeding stations and the N.I.A.B., seed certification schemes have been developed on a voluntary basis. These schemes aim at the preservation of varietal purity at a high level and the exclusion of seed-borne diseases and pernicious weed seeds.

Various schemes have been developed which are based on some or all of the following 5 principles :—

(1) Use of proved stock seed only. Sowings have shown that this is the most important principle and the development of vegetative propagation is proving a substantial aid to stock seed production.
(2) Inspection and approval of the field before the seed crop is sown to ensure freedom from " Volunteer " plants derived from earlier cropping.
(3) Inspection and approval of the growing seed crop at critical stages in growth for genetic purity, isolation from other types which might inter-pollinate, and freedom from seed-borne diseases and pernicious weeds.
(4) Sampling and sealing of the finally cleaned produce.
(5) Growing the samples of seed stocks for comparison with the authentic type.

Attention is concentrated mainly upon those strains which have shown particular promise in trials throughout the country, or, for special purposes or regions. Some reduction in the number of strains being handled by seed growers is, in itself, an aid to securing authenticity and greater purity of type.

" Field Approval " schemes have been applied to some 75,000 acres of wheat, barley and oats and more than 400 private individuals have been trained and examined at Cambridge as approved inspectors. The scheme is based on principle (3) and to some extent principles (1) and (2) ; it is supervised by the N.I.A.B.

The scheme marks a considerable advance on former methods of choosing cereal seed in the corn exchange by hand samples which cannot be identified in variety or judged for the presence of diseases or pernicious weeds.

Field Approval Schemes for Aberystwyth and Corstorphine herbage strains are based on principles (1), (2) and (3).

Comprehensive certification schemes for herbage seeds grown in the three counties of Lincolnshire, and in Wiltshire, Hampshire and Dorset, are based on all five of these principles. " Growing-on " tests have shown that the sealed bags contain seed of high varietal purity substantially free from pernicious weed seeds.

Vegetable seed stocks are now being developed under a co-operative scheme of the National Vegetable Research Station, the Seed Trade Association and the National Farmers' Union working in conjunction with the N.I.A.B. ; this scheme depends for its value on principles (1), (4) and (5).

Economics must influence the choice of a suitable scheme. Crops such as broccoli and sprouts where the cost of seed normally constitutes only about 3 to 5 per cent. of the cost of growing the crop, justify a scheme which includes the sampling and sealing of packages and the growing of samples of seed.

Cereal seed which already represents about 15 per cent. of the cost of growing the crop owing to the much slower rate of reproduction cannot easily bear the cost of operating principles (2), (4) and (5). But stock seed of cereals direct from the plant breeding stations multiplied at the N.I.A.B. and by the Welsh Seed Growers' Associations merits the application of the full range of principles (1) to (5) so that the highest quality seed may be obtained for further multiplication.

A practical difficulty of seed certification schemes with vegetable seeds is that these are sold mainly in small packets and the seedsmen must be able to divide the original sealed bags. For the protection of all parties concerned the Swedish system of spraying certified seed with a substance which can be identified has

much to commend it. A similar problem arises in the case of herbage seeds which are normally portioned out so that they may be mixed with other species in a form ready for sowing.

To meet, adequately, the need for bigger and more consistent yields of food crops it is essential to have a very clear understanding of the principles which influence the reproduction of improved stocks, an objective and experimental approach to the problem and the fullest utilisation of trained personnel at all stages of production.

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BREEDING FOR YIELD IN THE CEREALS

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There are two distinct methods of breeding for yield which Frankel describes as " overcoming limiting factors " and " assembling productivity genes." Examples of the former are breeding for disease and frost resistance. These methods are generally straightforward since the breeder has visible characters on which to select. The second method is more difficult, since advances may not become apparent until the selections have been tested for some years. The breeding systems in common use in hybrid cereal populations are based on two methods, neither of which is well suited for the study of quantitative characters. In the Pedigree Method about 95 per cent. of the plants in the segregating generations are thrown away each year, purely on eye judgment. In the Population Method about 95 per cent. of the seed is discarded each year purely at random. Natural selection favours those lines capable of most rapid multiplication under conditions of competition. In both methods high yielding lines may be discarded because there is no way of recognising them.

Trials of unselected crosses.—The Population Method may be modified by growing the early generations of unselected crosses in trial for yield comparisons either of different crosses or of different generations of the same cross. The early generations normally show heterosis ; their yields sometimes exceeding that of the mid-parent by as much as 30 per cent. The amount of this excess may indicate the number of yield genes and, therefore, the possibility of selecting high yielding pure lines. Provided that no selection has occurred, the amount of this excess should be approximately proportional to the amount of heterozygosity remaining in the stock. Thus it will be halved at each generation so that hybrid and mid-parental yields will become equal when homozygosity is achieved. In trials of this type at Cambridge it is noticeable that winter wheat crosses have given much higher yields than spring wheat crosses relative to their respective parents. This may be due to segregation of the latter into early and late maturing types followed by natural selection against the late plants. This would invalidate the method since the absence of selection is an essential condition.

Trials of F_2 progenies.—The Pedigree Method may be modified by limiting selection to the F_2 and F_3 generations and then growing the progenies of selected F_3 plants in trial in F_4 and later generations. Finally, single plant selections must be made within the high yielding progenies, as it has been shown that these contain more

and better high yielding lines. The weakness of the method lies in the small number of progenies which can be adequately tested, although the use of cubic lattice designs may help. It is most applicable where F_2 and F_3 selection can be very intense thus reducing the number of progenies to be tested.

Analysis of single plants.—The yielding ability of a wheat variety is the product of the average values of grain weight and numbers of grains/spikelet, spikelets/ear, ears/plant and plants/unit area. Varieties owe their yield to different combinations of these five characters. In a hybrid population yielding ability can be estimated by measuring these characters and calculating a discriminant function in which each character is weighted according to the contribution it makes to yield. Then by applying these coefficients to the original single plants each can be assigned a score representing its yielding ability. A disadvantage of this method is the long time required to make the measurements and calculations. In analyses of spring wheats made at Cambridge, one F_2 showed a 10 per cent. increase in number of spikelets per ear compared with the mid-parent. Presumably, if the other characters had also shown increased values, the possibility of selecting a high yielding line would be greater. Thus crossing two varieties owing their yield to a high expression of different characters may be more productive than merely crossing the highest yielding varieties.

Small scale yield trials. Yield differences of the order of 5 per cent. are frequently not significant even in field-scale trials. Breeders' trials, especially in early generations, are likely to be limited in size by the amount of seed available. It is, therefore, important to consider how this seed may best be used. A dibbed trial with spaced plants is the most economical way of using seed, but the effects of varying seed rate are still obscure. A comparison of two 6×6 Latin Square trials of barley, one drilled and the other dibbed showed that the drilled trial had a higher standard error, and also that the range of varietal yields was much greater. This more than compensated for the higher standard error with the result that the drilled trial was significant, whereas the dibbed one was not. The order of magnitude of the varietal yields was, however, virtually the same for the two trials. Other evidence suggests that the order of yields is sometimes inverted when changing the method of sowing. It seems possible, therefore, that the dibbed trial, which is essential if individual plants are to be studied, may give a wrong estimate of yield. This subject is now being investigated further at Cambridge.

VARIETY TESTING

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The subject of variety testing has been discussed at two previous conferences (1948 and 1949) and on the last occasion it was recommended that a small Committee be set up by the A.R.C. to consider the question in all its aspects. On this occasion it is possible in the time available to introduce only one point, and the suggestion is made that there is need for facilities for the plant breeder to test and select from breeding material in its early stages, while it is still variable, so that advantage can be taken of the reaction of heterozygous material to a wide range of conditions throughout the country. The testing of varieties or strains considered by the breeder to be highly promising is already well catered for by the N.I.A.B. and its chain of substations, but by the time the material reaches the trial plots of the N.I.A.B. it is a potential new variety. It is not generally possible to select at one centre for all climates and soils, and the wider testing, at an earlier stage, of more-heterozygous material may well lead to the ultimate selection of more than one variety. Two objections may be raised at once.

(*a*) that far too much work and organisation would be involved. It is suggested that trials of this kind over only a few years would indicate in which areas there were radical differences of environment which called for special

attention and the number of trial areas could thereafter be reduced; and that in these exploratory stages, it should not be essential to have to establish new stations for the purpose—use could probably be made of existing facilities; or alternatively that a modest start could be made with existing facilities and the idea extended when it had proved its usefulness.

(*b*) that there are already too many varieties. Paradoxical as it may seem, a method such as is now suggested may well lead to a *reduction* in the number of varieties in use, since the intending grower could use a variety bred for his area instead of trying a random sample of the hundreds now on the market in the hope of finding one to suit his conditions.

The method used in the Commonwealth should be applicable, whereby hybrid material was sent out in early stages (F_2 onwards) for small-scale trials and selection; the field work was done by the man on the spot, but selection done by the breeder at HQ who worked with that particular crop or group of crops and who travelled around during breeding season. The N.V.R.S. have been offered facilities at the N.A.A.S. Experimental Horticulture Station, which it is proposed to use for the testing of this more-variable breeding material; these stations are yet few, but it is proposed to begin in the hope that it will later be possible to expand. The testing of potential new varieties will continue to be done by the N.I.A.B.

NEW TECHNIQUES IN PLANT BREEDING

W. J. C. LAWRENCE
John Innes Horticultural Institution, Bayfordbury

Recently a variety of new aids to plant breeding have been developed which will make for better control, greater ease and speedier results.

The supplementary artificial illumination of seedlings is an example. By its use the quality of seedling growth is greatly improved in winter time (October-March), the rate of development is accelerated and plants come into flower and fruit earlier, thus making possible the raising of one or more generations per year. Artificial light can also be used to advance or retard the time of flowering in many species, a photoperiodic effect which is additional to that mentioned above for seedlings. The use of artificial light for photosynthetic and photoperiodic control is in its infancy, but clearly it provides a powerful tool for the plant breeder.

Temperature control is another promising aid. Already temperature and light control have been used to secure the flowering of biennial plants, such as beet and onions, in the first year, also for the selection of male plants in asparagus.

On the mechanical side there are a number of new aids. First, there is the electric "bee" for rapid and efficient pollination and the collection of pollen. Next, liquid air seems to offer considerable scope in the storage of pollen. Thirdly, use is made in Holland of certain wild queen bumble bees for the pollination of brassicas in insect-proof cabinets. These bees have diseased sexual organs (the result of nematode infestation) and consequently do not attempt to "home". They are caught by trained observers who identify them by their erratic flight. Much tedious work could be avoided by using such bees, especially where the flowers are small and difficult to manipulate.

Another aid developed in Holland is the "Dutch Light" structure, consisting of frame lights fixed to a metal or timber framework. This structure provides at small cost protection from wind and rain and can be readily adapted to provide controlled air and soil temperatures together with photoperiodic light control. The mobile glasshouse running on rails is another aid which deserves the attention of the breeder, especially for the maturing of crops and seed. Unfortunately almost all of these aids are only to be seen abroad, and one wonders if the camel-hair brush and forceps have not already become the insignia of the British plant breeder.

GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers read at the HUNDRED AND TENTH MEETING of the Society, held on 8th NOVEMBER 1952, at the GALTON LABORATORY, University College, London, W.C. 1

THE GENETICS OF HUMAN BIRTH WEIGHT

ELIZABETH B. ROBSON
Galton Laboratory

A large series of birth weights of normal infants collected in the Galton Laboratory had been used to estimate the effect on the fœtus of maternal age, parity, duration of gestation, and sex. In the present investigation family material was collected for genetical analysis. The statistical technique of correlation was used to test various hypotheses regarding the inheritance of birth weight. On the hypothesis that the birth weight of an infant is determined through its own genotype, by multiple factors without dominance or sex-linkage, the expected sib-correlation is 0·5 and that between first cousins 0·125. The results obtained by a preliminary analysis confirmed the sib-correlation of about 0·5 found previously. A positive likeness of birth weight in children of sisters was demonstrated, but not in other types of cousins. This would seem to indicate that the genotype of the fœtus is of less importance in determining its own birth weight, than a maternal characteristic which shows similarity among sisters. Analysis by a more refined method is now being undertaken.

LINKAGE STUDIES IN THREE FAMILIES SHOWING OVAL RED CELLS (ELLIPTOCYTOSIS)

SYLVIA D. LAWLER
Galton Laboratory

Three families showing the oval red cell anomaly have been investigated (Family 1 by Dr H. Lowenthal, Family 2 by Dr J. N. M. Chalmers and Family 3 by Dr H. Goodall). Members of these families have been blood typed by the author. There is evidence that the gene determining the oval red cell anomaly is on the same chromosome as the genes of the Rhesus blood group system. The families considered together provide an illustration of the problems involved in human linkage investigations.

TWO BLOOD GROUP ANTIGENS IN AFRICANS, ASSOCIATED WITH THE MNSs SYSTEM

J. N. M. CHALMERS
St George's Hospital, London
ELIZABETH W. IKIN and A. E. MOURANT
Medical Research Council Blood Group Reference Laboratory

A study has been made of the distribution among West Africans, and of the genetics, both of the newly-detected Henshaw antigen and of the Hunter antigen previously described by Landsteiner, Strutton and Chase (1934, *J. Immunol.*, *27*, 469). The Henshaw antigen has a frequency of 2·7 per cent. and the Hunter antigen one of 22 per cent. among unselected West Africans. The genes for both of these antigens are closely linked to those for the MNSs system, the Henshaw gene being almost invariably attached to an NS chromosome and the Hunter gene to Ns.

INTERSEXUALITY IN *DROSOPHILA SUBOBSCURA*

HELEN SPURWAY and J. B. S. HALDANE
Department of Biometry, University College, London

No abstract.

INCOMPATIBILITY IN *PTERIDIUM AQUILINUM* (BRACKEN)

D. WILKIE
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It was found that individual prothalli isolated before the formation of sexual organs do not usually produce sporophytes at maturity, whereas mass-cultured prothalli do.

Sexually immature prothalli were isolated in pairs and singly, respectively, in phials and periodically flooded with water after maturity. Of 19 isolated prothalli, none produced a sporophyte but 9 out of 18 of the paired prothalli did, both members of each of the nine pairs producing a sporophyte in each case.

Clones of prothalli were produced by sectioning individual prothalli. Of 14 clones tested against a fifteenth clone, 4 showed compatibility both when used as male or female parent. Tests of 3 of the 14 clones against one another gave the expected results.

The spores used in all these experiments came from a single frond of a particular population. Apparently this is the first recorded case of incompatibility in the Pteridophytes.

PAPER ELECTROPHORESIS OF HÆMOLYMPH FROM NORMAL AND MUTANT *DROSOPHILA* LARVÆ

H. GLOOR and CH. WUNDERLY
Zoology Department and Medical Clinic, University of Zürich

With the purpose of detecting biochemical differences between wild type and certain mutant types in *Drosophila*, paper electrophoresis of the proteins of hæmolymph was undertaken. In two experiments hæmolymph was obtained from full-grown larvæ of two lethal mutant types (*ltr*—lethal translucida of *D. melanogaster*, *lpl*—lethal polyploid of *D. hydei*) and their respective wild types. The larvæ were punctured individually on a siliconised slide and extruded fluid was sucked up in a capillary pipette. Amounts of this fluid in the range of 0·075 to 0·30 ml. were placed on paper and subjected to electrophoresis by a 9mA current, 135 Volts (veronal buffer of *p*H 8·9) during 10 to 15 hours. Bromophenol blue treatment revealed at least two distinct proteins, both with electrophoretic mobilities in the range of the alpha and beta globulins of human blood serum. Thus it was shown that *Drosophila* hæmolymph contains at least two protein fractions easily separable by this method, in contrast to tissue protein mixtures. In both species the hæmolymph from the lethal larvæ contained essentially the same proteins as that from the corresponding normal type. Quantitative differences however seemed to be indicated.

INHERITANCE OF WHITE IN THE "ENGLISH" RABBIT

E. C. RICHARDSON
Ecclesbourne, West Byfleet

The English rabbit of the Fancy is heterozygous for self-colour and for "Charlie Chaplin". The white of the "Charlie" is sub-lethal. It varies greatly in degree of expression owing, presumably, to modifying genes. Thus it is possible to produce heterozygotes of a degree of whiteness comparable to that of the homozygote, even to the extent of showing the typical "moustache" of the "Charlie". This supports Haldane's theory of the origin of dominance.

LINKAGE VALUES FOR *POLYDACTYLY* AND *LEADEN*

SIR RONALD FISHER
Department of Genetics, University of Cambridge

A short note on these linkage values.

DISTRIBUTION OF GENE FREQUENCIES IN *TRIFOLIUM REPENS* L.

H. DADAY
Welsh Plant Breeding Station, Aberystwyth

The cyanogenetic glucoside and enzyme genes were investigated in wild white clover populations of Europe and the Near East, including Alpine populations, and cultivated strains. Four chemical phenotypes of plants were distinguished as follows :—(1) Glucoside and enzyme (G+E), (2) Glucoside only (G), (3) Enzyme only (E), (4) Neither glucoside nor enzyme (O) phenotypes. The gene frequencies of populations were determined by the Hardy-Weinberg formula $(p^2+2pq+q^2=1)$.

A very great variation was disclosed in the occurrence and the proportion of the four phenotypes in populations from different parts of Europe and the Near East. A transformation in the phenotypic structure of populations became evident, and the tested sample revealed a change from south to north-east. A continuous gradual decrease of the dominant cyanogenetic glucoside and enzyme gene frequencies was established within a range of 100 per cent. The dimunition in dominant gene frequency was found to be very closely correlated with January isotherms.

A similar change in the phenotypic structure and of decreasing gene frequency was found in Alpine populations. The cultivated white clover shows a similar phenotypic and genotypic structure to the wild populations from where they derived, but a certain divergence was revealed in genetical structure owing to the selection practised by the breeder.

EQUILIBRIUM OF POPULATIONS AND THE POSSIBILITY OF SUSTAINED LARGE-SCALE OSCILLATIONS

A. R. G. OWEN
Department of Genetics, University of Cambridge

In most of the cases where a set of genes is supposed to be under natural selection in a population, it is found that the population will tend to a stable equilibrium state, which is either trivial or non-trivial. (A trivial equilibrium is achieved by entire extinction of some genes.) Haldane has indicated the possibility of more than one stable equilibrium for m unlinked loci, and in tetrasomics. Few cases, if any, seem however to have been treated in detail.

I have therefore constructed some interesting theoretical populations. One of them shows *two* stable equilibria, the initial conditions determining which one is attained. Another population which I have discussed is less likely to be realised in nature, but settles a question of principle because it has *no* stable equilibria at all. It progresses through an endless succession of widely differing states in an almost periodic motion, performing perpetual oscillations of large amplitude. It can reach a limiting state only by *random* extinction of a gene, so that its final state is highly indeterminate. I have also discussed equilibrium of three alleles, deriving new relations between viabilities of the heterozygotes and the homozygotes, which are verified by Dobzhansky's observations.

A SUPPRESSOR IN *CHLAMYDOMONAS REINHARDI*

J. N. HARTSHORNE
Botany Department, University of Leeds

Following ultra-violet irradiation of the heterothallic, unicellular alga *C. Reinhardi*, a mutant was isolated which lacked the eyespot. This mutant (" eyeless ") was crossed with the wild-type, and the progeny from each zygote analysed showed regular 1 : 1 segregation for presence or absence of the eyespot. The same progenies also segregated for two characters affecting colony size, which were named " small-colony " and " slow-growth ". Both these characters appeared to be due to single genes which were suppressed by the wild-type allele at the eyeless locus and were expressed only in the presence of eyeless. The origin of these characters is obscure. If, as appears likely, the genes concerned were present in the wild-type stocks in a suppressed condition, the eyeless mutant would have been expected to manifest both characters when it first arose. Yet in the appearance of the colonies, the original eyeless strain was indistinguishable from wild-type.

GENETIC CONTROL OF INFLORESCENCE DEVELOPMENT IN *LOLIUM*

J. P. COOPER
Department of Agricultural Botany, University of Reading

In the genus *Lolium*, the annual species of Mediterranean origin, *L. rigidum* and *L. gaudini*, have a low critical photoperiod (below 9 hours) and form heads rapidly without exposure to low temperature. The perennial herbage strains of *L. perenne* from N.W. Europe will not form heads without low temperature exposure and have a high critical photoperiod.

In crosses between the ecological extremes (*L. rigidum* and a pasture strain of *L. perenne*), response to both low temperature and photoperiod shows polygenic control. The underlying variate of response is distributed normally in each case, but if the distribution overlaps a threshold level, resolution into heading and non-heading plants occurs. Each outbreeding population of *L. rigidum* or *L. perenne* although phenotypically uniform in heading behaviour under the conditions for which it has been selected, is far from uniform genetically. Genetic variability in response to low temperature and photoperiod is carried both between apparently similar plants, and also within plants in the heterozygous condition. This genetic variability is uncovered when either a sample of the population, or progenies from selfing individual plants, are grown under threshold temperatures or photoperiods. No such genetic diversity is revealed within single lines of the inbreeding species *L. temulentum*.

EUPHYTICA

NETHERLANDS JOURNAL OF PLANT BREEDING

This new and valuable journal has recently appeared. Three parts are to be issued annually. Volume 1 (1952) is now complete. It contains, in English and Dutch, original articles on plant breeding, summaries of papers read at the meetings of the Netherlands Study Centre of Plant Breeding, and English abstracts of articles published in Dutch. The annual subscription is 15 guilders (about 30s. or $4) and the managing editor is Dr H. de Haan, Nude 66, Wageningen.

PROFESSOR OTTO RENNER

We offer our congratulations to Professor Otto Renner, Director of the Botanical Institute of the University of Munich on celebrating his 70th birthday, 25th April 1953.

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